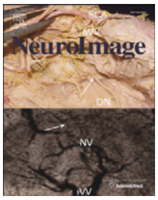
NeuroImage 60 (2012) 1925–1936

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Delayed monitoring of accuracy errors compared to commission errors in ACC

Benoit Bediou [a,b,*], Leonie Koban [a,c], Sébastien Rosset [a,b], Gilles Pourtois [d], David Sander [a,b]

[a] *Swiss Center for Affective Sciences, University of Geneva, Switzerland*
[b] *Laboratory for the Study of Emotion Elicitation and Expression, University of Geneva, Switzerland*
[c] *Laboratory for Neurology & Imaging of Cognition, Neuroscience Center, University of Geneva, Switzerland*
[d] *Department of Clinical Experimental & Health Psychology, Psychopathology and Affective Neuroscience Lab, Ghent University, Belgium*

ARTICLE INFO

Article history:
Received 9 November 2011
Revised 19 January 2012
Accepted 4 February 2012
Available online 14 February 2012

Keywords:
Error-related negativity
GO-NOGO
Prediction error
Feedback
ACC

ABSTRACT

Error detection is essential for monitoring performance and preparing subsequent behavioral adjustments, and is associated with specific neural responses in the anterior cingulate cortex (ACC). To investigate whether different brain mechanisms subserve the processing of commission vs. accuracy errors, we recorded EEG in adult participants while they performed a novel speeded GO-NOGO aiming task (*"the Shoot-NoShoot paradigm"*). Our ERP results show that commission errors (responding during NOGO trials) elicited a classical error-related negativity (ERN) component, followed by an error-related positivity (Pe), as well as a negativity peaking before response onset (pre-ERN). By contrast, spatial accuracy errors elicited a feedback-related negativity (FRN), which correlated with the spatial discrepancy between response and target position across subjects. Fast hits also elicited a pre-ERN but no ERN, suggesting that this pre-response monitoring component might be related to the detection of error likelihood. Although source analysis revealed similar generators in ACC for these different error-related negativities, the respective timing differed, suggesting that commission errors are detected rapidly based on internal motor representations, whereas the detection of accuracy errors in ACC relies on the additional and swift processing of external visual information.

Introduction

In order to reach goals, humans have to constantly monitor the outcome of their behavior. Accordingly, they have to detect deviations from intended actions and outcomes, which can be due to various types of action errors. If you play dart in the local pub, and your goal is to win, you have to shoot at the right moment (when it is your turn), as well as to concentrate and aim at the center of the dartboard usually providing the highest reward. When the dart hits the board, you can evaluate the outcome of your trial, i.e., how many points you have gained. Obviously, you can fail during different stages of this process, based on different types of errors or noise: if you shoot while someone is passing between you and the dartboard, this can be seen as an error of commission. If you shoot at a good moment, you still can miss the goal, because of erring in accuracy likely resulting from an inappropriate motor planning or command.

The goal of this study was to compare, using scalp EEG measurements in healthy participants, the electrophysiological correlates of these two different error types, commission vs. accuracy errors, which differ from one another with respect to several key aspects: First, commission errors usually reflect an inhibition failure, whereas accuracy errors may be due to sub-optimal action execution or motor planning. Second, commission errors are usually "qualitative" (i.e., all-or-none), whereas accuracy errors are quantitative in nature (i.e., sizable). Third, the detection of commission errors might already occur during motor execution, whereas the detection of accuracy errors is usually based on a rapid evaluation of the outcome (i.e., when directly seeing the position reached on the dartboard and comparing it with the aimed position).

Previous EEG research has already characterized several event related brain potential (ERP) components related to error detection and performance monitoring. The error-related negativity (ERN) is a negative potential with a frontocentral distribution that is elicited within 0–100 ms following the commission of a response error (Dehaene et al., 1994; Falkenstein et al., 1991; Gehring et al., 1993). The feedback related negativity (FRN) is a topographically similar negativity peaking ~150–300 ms following the presentation of a negatively-valenced visual feedback, such as performance feedback indicating an error (Luu et al., 2003; Miltner et al., 1997; Stahl, 2010), or a utilitarian feedback reporting a monetary loss (Gehring and Willoughby, 2002; Hajcak et al., 2006; Nieuwenhuis et al., 2004b; Yu and Zhou, 2006).

Source localization results point to the dorsal anterior cingulate cortex (dACC) as the main generator of both ERN (Dehaene et al., 1994; van Veen and Carter, 2006; Yeung et al., 2004) and FRN (Miltner et al., 1997), and the implication of the dorsal ACC in error detection (and correction) has been confirmed with various neuroimaging techniques, including functional magnetic resonance imaging

---

[*] Corresponding author at: Benoit Bediou, Brain and Learning lab, University of Geneva, Boulevard pont d'Arve 40, CH-1205 Geneva, Switzerland. Fax: +41 22 379 90 20.
E-mail address: benoit.bediou@unige.ch (B. Bediou).

1053-8119/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2012.02.010

(fMRI, e.g., Debener et al., 2005; Holroyd et al., 2004), magnetoencephalography (MEG, e.g., Keil et al., 2010; Miltner et al., 2003), and intracranial recordings (Brazdil et al., 2002, 2005; Emeric et al., 2008; Halgren et al., 2002; Niki and Watanabe, 1979; Pourtois et al., 2010; Wang et al., 2005).

The ERN, which is thought to index an early (perhaps automatic) stage of error detection (Nieuwenhuis et al., 2001), is generally followed by the error positivity (Pe) peaking ~150–200 ms after an incorrect response over central electrodes (Falkenstein et al., 1991). The Pe has been associated with the conscious detection of an error (Dhar et al., 2011; Ridderinkhof et al., 2009; Steinhauser and Yeung, 2010) and the engagement of remedial actions. Even though these ERP studies provide only indirect evidence regarding the actual involvement of specific brain structures during error monitoring, interestingly, the Pe component was also found to be generated in the ACC, though its sources were usually found either more rostral (Herrmann et al., 2004; Shalgi et al., 2009; van Veen and Carter, 2002), or more caudal (Falkenstein et al., 2000; Vocat et al., 2008), than the generators of the ERN in this medial frontal region.

The reinforcement learning (RL) theory holds that the ERN and FRN indirectly reflect activity of a deep mesencephalic system projecting to the basal ganglia and then the ACC, where these ERP responses are eventually generated (Frank et al., 2005; Holroyd and Coles, 2002; Nieuwenhuis et al., 2004a). According to this model, neurons in the basal ganglia constantly monitor ongoing behavior. Errors, negative feedback, and other worse-than-expected events induce a phasic decrease in the activity of these neurons (see Fiorillo et al., 2003), thereby generating a prediction error signal that is conveyed to the dorsal ACC (which is the putative generator of the ERN or FRN component), leading to adaptive changes in action selection (Rushworth and Behrens, 2008).

A main prediction of the RL theory is that only the earliest predictor of incorrect performance will generate an unequivocal error signal. Hence, an ERN or an FRN component is generated depending respectively on whether internal information (i.e., response) or external information (i.e., feedback) is the “first indicator” of an unfavorable outcome, a hypothesis that has received direct empirical support (Gentsch et al., 2009; Heldmann et al., 2008; Krigolson et al., 2009; Staedtgen et al., 2000; Stahl, 2010). To put it simply, the RL theory predicts that errors which can be detected on the basis of internal (motor) information elicit an ERN following the response but no FRN following the feedback, whereas errors which cannot be detected based on the internal motor command and require the processing of an external signal elicit an FRN following negative performance feedback, but no ERN following the response (Eppinger et al., 2008).

Another ERP component sensitive to errors, the pre-ERN (pre-error negativity), has been described more recently by Ruiz et al. (2009). These authors recorded ERPs in expert pianists while they performed a memorized music piece at fast tempo in the presence vs. absence of auditory feedback. They observed a medial frontocentral negativity that shared the same electrophysiological characteristics as the ERN but occurred 70 ms before a wrong note was played by the pianist. Because pianists anticipated several notes during motor preparation, these authors suggested that the pre-ERN could reflect the ability of the action-monitoring system to anticipate an upcoming error based on a temporal prediction error signal (or alternatively, corollary discharges generated from premotor regions) operating before the onset of this action, here a wrong note hit by the pianist. Although this ERP component has not been interpreted within the framework of the RL theory, the pre-ERN may reflect an error at the level of motor preparation, i.e., a prediction error between the intended motor response and the actual motoric task goal.

To address the question whether the detection of commission errors and accuracy errors share similar brain mechanisms, we designed a novel speeded GO-NOGO aiming task that is suited to elicit and directly compare different types of errors within the same participants, while EEG is concurrently recorded. Participants were instructed and trained to use a light-gun response device to “shoot” as fast and accurately as possible on visual targets appearing at one of eight possible screen locations, while avoiding shooting predefined non targets. In this task, commission errors are due to incorrect responses (i.e., false alarms, FAs), whereas accuracy errors result from inaccurate responses (i.e., missed targets).

To test the predictions derived from the first indicator hypothesis of the RL theory, a visual feedback timely indicating the spatial position of the response with respect to the stimulus was delivered synchronously with the response. This response feedback is not “evaluative” per se, as the subject needs to perceive that there is either a match or a mismatch between the position of this immediate visual feedback and the target position to eventually infer whether his action is correct or not. A second and informative performance feedback indicating the correctness of the response was provided only 1000 ms after this immediate response feedback. We surmised that for commission errors, an internal representation of the response may be sufficient to detect whether the action is correct or not, such that an ERN (and possibly subsequent Pe as well as antecedent pre-ERN) should be elicited following these commission errors. In this case, the response feedback (i.e., the online display of the spatial position of the gun shot) should not be informative, and no FRN should be elicited, because the feedback provides redundant monitoring information. By contrast, for accuracy errors, the response is presumably not sufficient in itself to assess the correctness of the action. Hence, in this condition (accuracy errors), a FRN component should be elicited as the participant presumably needs to process feedback information in order to detect whether his action is correct or not. In addition, we predicted that the amplitude of this FRN component generated following accuracy errors could actually vary with the magnitude of the perceived discrepancy between the spatial position of the shot on the screen and the location of the actual target (i.e., the larger this spatial deviation, the larger the amplitude of this error-related activity), in keeping with previous ERP results that already reported such parametric association for the ERN component during a simple visuo-motor pointing task (Vocat et al., 2011).

Material and methods

Subjects

Twenty healthy male students from the University of Geneva (mean age 22.8, SD = 4.8 years-old) participated in this study in exchange of 15 CHF payment, plus a bonus depending on performance (accuracy and RT, see Table 1). The average bonus was 7.75 CHF (SD = 2.07, range 4–12). Participants were all right-handed and used their dominant hand to respond. None of them had a history of neurological or psychiatric disorder, and all participants were free of any medication at the time of testing. EEG data from one subject

Table 1
Bonus schedule.

1a) Performance bonus

Accuracy (%)	<50	50–59	60–69	70–79	80–89	90–100
Amount (CHF)	0	1	2	3	4	5

1b) Reaction time bonus

RT (ms)	>550	450–550	350–449	250–349	<250
Multiplier	x 0	x 1	x 2	x 3	x 4

Note. Participants received a fix amount (15 CHF show-up fee) plus a bonus which was determined by both accuracy and speed. Performance defined the amount and reaction time a multiplication factor (range 0–20 CHF). For example, an average score = 63% with an average RT = 335 ms resulted in a 6 CHF bonus.

could not be recorded due to technical problems with the EEG amplifier.

Stimuli and task

Our task is an adaptation of the standard GO-NOGO paradigm. We used simple color geometric shapes as visual stimuli. For half of the participants, a yellow triangle corresponded to the imperative GO stimulus while a yellow circle and a blue triangle were associated with NOGO responses. Compared to the GO stimulus, the NOGO stimulus had either the same color but a different shape (shape NOGO), or the same shape but a different color (color NOGO), enabling two NOGO types. To control for differences in low-level visual features between the stimuli, the mapping between color/shapes and GO/NOGO was counterbalanced across participants. Hence, for the other half of the participants, the GO stimulus was a blue triangle while the NOGOs were the yellow triangle and blue circle, respectively. Participants were instructed to respond to GO stimuli but to withhold responding to NOGOs. The experiment consisted of 4 blocks of 96 trials each comprising 64 GOs and 32 NOGOs (16 shape-NOGO trials and 16 color-NOGO trials) presented in random order. Subjects responded with a light-gun device similar to those used in a number of video games (www.hkems.com/product/xbox/LCDTopGun.htm).

The visual stimulus (either a GO or a NOGO) appeared at one out of eight possible positions around a central fixation cross (Fig. 1). The eight possible stimulus locations were indicated by squares of 180 × 180 pixels in size and remained on the screen for the duration of a block. These “boxes” were aligned horizontally and vertically and placed at 25%, 50% and 75% of the screen's width and height, subtending a maximal visual angle of 6.9 × 5.5°. There was no box in the center of the screen (50% on both x and y axis), where the central fixation cross appeared. The geometric shapes were 180 pixels in width and 290 pixels in height and were stretched to fit in the boxes. Stimulus presentation was semi-randomized, such that each stimulus type appeared equally often in each of the eight possible positions. Accordingly, the different trial types were defined as follows: A GO trial was counted as correct (and a NOGO incorrect) if the participant's response fell inside the square containing the stimulus (even if the response was inside the square but outside the stimulus). Hits were defined as correctly aimed GO trials within the time limit. Correctly aimed GO trials that occurred outside the time limit were counted as RT errors and were not analyzed. Accuracy errors corresponded to gunshots made on GO trials within the time limit but eventually falling outside the relevant box containing the aimed GO stimulus. Commission errors corresponded to accurate gunshots (i.e., reaching the aimed box containing the relevant NOGO stimulus) made on NOGO trials within the time limit. Thus, two different types of error were obtained with this task: commission errors corresponded to trials in which participants responded to a NOGO stimulus (i.e., incorrect decision and action), whereas accuracy errors corresponded to

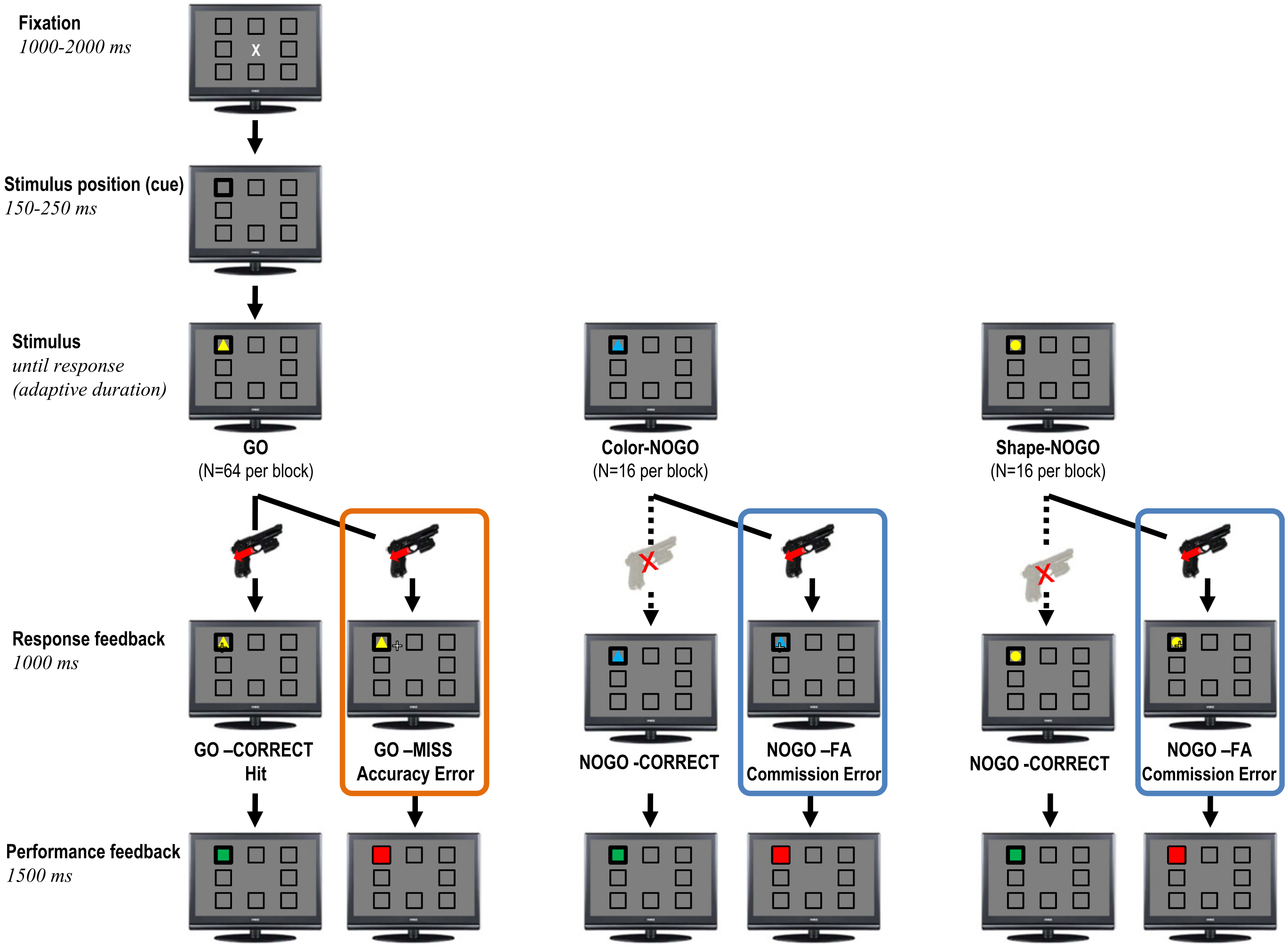


Fig. 1. Description of GO and NOGO task trials from the shoot–noshoot paradigm. Note. There is no delay between response and response feedback. ERPs are time-locked to the onset of the response, which coincides with the response “feedback” (i.e., “+” sign indicating the position aimed with the gun on the screen). The performance feedback (i.e., correct or not) is given 1000 ms after the response feedback (ERP data not shown here).

trials in which participants responded on a GO stimulus but actually missed the target position (i.e., correct decision to shoot but inappropriate action leading to a missed target). Importantly, for errors of decision, only correctly aimed NOGOs were counted as incorrect. Responded but missed (i.e., inaccurate) NOGOs were counted as correct and were associated with a particular feedback (“CAUTION!”). As it turned out, the number of inaccurate NOGO trials was not sufficient to compute reliable ERP waveforms in this condition for each participant.

A task trial consisted of the following sequence of events (Fig. 1). A central fixation cross (1000–2000 ms) indicated the beginning of a trial. We used a different sign to avoid confusion between fixation (“x”) and online visual feedback of aiming position of the gun on the screen (“+”). Then, the central fixation cross and the feedback of the aiming position disappeared, and the outer border of one of the 8 boxes was thickened (150–250 ms), indicating the position (but not the type) of the forthcoming stimulus (i.e., cueing). Then, a GO or NOGO stimulus was displayed in this (previously highlighted) box until a response was recorded or until the adaptive time limit was reached, except for correct NOGOs (see below). Immediately after the response, the “+” sign appeared again to indicate the position of the shooting response (1000 ms). Hence, as soon as they responded, the exact position of their shot, and thereby the inferred magnitude of any potential accuracy errors, was “quasi immediately” made (implicitly) available to participants. Finally, a performance feedback (1500 ms) indicated whether the response was correct (the box turned green, with the word “CORRECT” displayed in the center of the screen) or incorrect (the box turned red and the word “FALSE” was displayed in the center of the screen), before the fixation cross appeared again, indicating the beginning of the next trial. Correctly aimed GOs (hits) within the time limit and non-responded NOGOs were counted as correct. Missed GOs (accuracy errors), slow GOs, non-responded GOs (RT errors), and correctly aimed NOGOs (commission errors), were classified as incorrect. Other feedback displays were used when subjects were too slow on GO trials (the box turned orange and the text “TOO SLOW!” was displayed in the center of the screen) or when they responded but missed a NOGO (the box turned orange and the text “CAUTION!” was displayed in the center of the screen).

We used two different procedures to increase error commission. To increase the number of accuracy errors, the “+” sign showing the aimed position on the screen was shown only between but not during trials (Fig. 1). To increase the number of commission errors, we introduced time pressure using an adaptive time limit for the duration of the stimuli and thus the recording of participant's responses. This adaptive time limit concerned GO trials only, all NOGO stimuli were displayed for 1000 ms, except for commission error trials. The duration of the GO stimuli was adapted on each trial according to performance (i.e., accuracy and speed). At the beginning of each block, the limit was set at 1000 ms. After each correct speeded GO response, a new limit for the subsequent trial was set to the average between the previous limit and the current reaction time (RT). By contrast, the limit was increased by 50 ms after each slow or non-responded GO, whereas it remained unchanged after each correct NOGO.

The participant's cumulative performance (percent correct responses) was continuously monitored and displayed at the bottom of the screen. For each block, performance started at 100% and decreased after each incorrect response (i.e., accuracy errors, commission errors, slow GOs and non-responded GOs). Conversely, cumulative performance increased (until 100%) after each correct response (i.e., hits, unresponded NOGOs and inaccurate NOGO responses). At the end of each block, participants received a detailed feedback of their average performance (accuracy and speed) for the whole block, as well as the RT for their best correct GO trial during this block.

To further increase their motivation and involvement, participants were informed that, in addition to the 15 CHF payment for their participation, they would receive an additional bonus which would depend on their best block performance using the payoff schedule as shown in Table 1. Average accuracy (percent correct responses) defined the amount of the bonus, whereas average speed (RT) determined a multiplication factor. The final bonus corresponded to the product of these two values. In addition to increasing participants' involvement in the task, this procedure ensured that errors were motivationally relevant and emphasis was placed on both accuracy and speed.

Before performing the task while recording EEG, participants went through two training sessions. During the first training session, an online feedback indicated participant's aiming position throughout the trial. As soon as participants reached 75% correct responses, the second training session began. This second session was similar to the first one, with the exception that the online visual feedback indicating the current aiming position (“+”) was visible only during fixation and after a response had been made (as done during the main EEG experiment).

EEG recording and processing

Subjects sat in a dimly lit sound-attenuated cabin, in front of a computer screen placed at a viewing distance of about 250 cm. In order to minimize movements and fatigue, participants were requested to keep their arms resting on a small table adjusted to their size (Fig. 2). The electroencephalogram (EEG) was continuously recorded at 2048 Hz with 64-channel (pin-type) Biosemi Active Two system (http://www.biosemi.com) referenced to the CMS-DRL ground (driving the average potential across the montage as close as possible to the amplifier zero). Details of this circuitry can be found on the Biosemi website (http://www.biosemi.com/faq/cms and http://www.drl.htm). The 64 electrodes were evenly distributed over the scalp using an elastic cap, according to the extended 10–20 EEG system. ERPs of interest were computed offline following a standard sequence of data transformation (Picton et al., 2000): (1) common average reference, (2) ocular correction for blinks (Gratton et al., 1983) using the electrode FP1, (3) −500/+500 ms epoching around the onset of the motor response (i.e., pressing on the trigger of the gun), (4) baseline correction (using the entire pre-response interval), (5) artifact rejection (average threshold 114.45, SD = 53.54 μV across participants), (6) averaging for each of the experimental conditions (hits, accuracy errors and commission errors, shape and color collapsed), and (7) 1–30 Hz digital filtering of the individual average data. Following this procedure, the mean number of trials per participant included in the ERP data was 125 (SD = 17, range 99–153) for hits, 45 (SD = 20, range 17–87) for accuracy errors, and 23 (SD = 12, range 8–49) for commission errors. Finally, subtraction waveforms were computed for each participant by removing

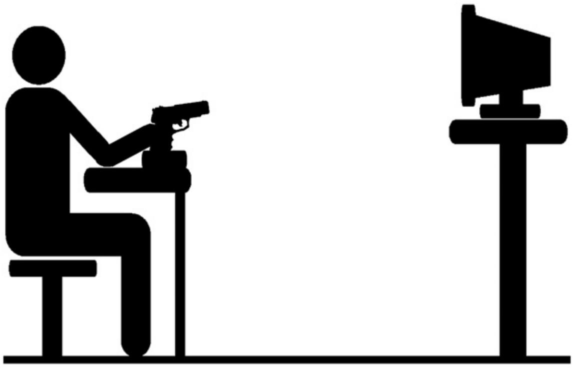


Fig. 2. Task setting.

correct trials ERP activities from error trials ERP activities, separately for accuracy errors vs. commission errors. This allowed us to (i) control for differences due to other processes than cognitive control or error monitoring (e.g. unspecific visual or motor effects), and (ii) determine the time windows of interest for further statistical analyses. Moreover, the pre-ERN, ERN and FRN components became more apparent when computing difference waveforms, although the pre-ERN may not be as sharp or phasic as the ERN or FRN component (e.g., Eichele et al., 2010). Importantly, statistical analyses were not run on amplitude values extracted from these difference waveforms, but instead, on the mean amplitudes of the individual averages before subtraction. While the ERN may be measured reliably using peak detection on the grand average ERPs, the pre-ERN and FRN have a more complex morphology, and are often seen as a relative negative deflection arising from a larger positive deflection. Therefore, the pre-ERN and FRN can be better identified using (error-minus-correct) difference waveforms, and accordingly they are also usually better characterized by mean amplitude measures. Thus, for each of these three ERP components (pre-ERN, ERN, Pe and FRN), we used a systematic and conservative data analysis based on mean amplitude measurements performed on the individual ERP averages, once the exact electrophysiological properties of these three consecutive action monitoring deflections (amplitude, latency and topography) had been clarified using grand average difference waveforms. Moreover, the use of mean amplitude measures for the pre-ERN, ERN, Pe and FRN is also compatible with previous ERP studies (e.g. Dhar and Pourtois, 2011; Potts et al., 2010; Ridderinkhof et al., 2003; Ruiz et al., 2009; San Martin et al., 2010; Yu and Zhou, 2009).

We first used the difference waves to define 4 time windows of interest, corresponding to the typical latencies reported for the pre-ERN, ERN, Pe and FRN components: −200 to −50 ms; 0 to 100 ms; 100 to 250 ms and 150 to 350 ms relative to onset of the motor response. Consistent with previous studies focused on these error-related ERP components (Overbeek et al., 2005; Vocat et al., 2011), we primarily focused on the electrode FCz, where these components were found to be maximal (see topographic maps in Fig. 5B). We first searched for the latency of maximum amplitude (either negative or positive depending on the component of interest) at electrode FCz during each time interval, for each condition and each subject separately, using the difference waveforms. We then calculated the mean amplitude of the individual averages (not difference waves) in a 20 ms time-window centered on each maximum or minimum, using the peak latencies from the grand average error-minus-correct difference waveforms. Thus, the difference waveforms were primarily used to determine the time windows for mean amplitude measurements in the individual averages, but the statistical analyses were conducted on mean amplitudes extracted from the individual average ERPs (i.e., not from the difference waveforms), following standard practice (Falkenstein et al., 2000).

Because the "+" sign (indicating the position aimed with the gun on the screen) was displayed again immediately following motor response, these ERP components (pre-ERN, ERN, Pe and FRN) likely reflected a combination of internal and external monitoring processes. More specifically, the FRN component found here was not elicited by the explicit visual performance feedback (given only 1000 ms following motor response), but by the spatial position sign, presented roughly at the same time as the response. Thus, the FRN may not correspond to a genuine feedback-related component. However, its polarity, latency, topography and sources were compatible with an FRN component (Miltner et al., 1997).

To clarify the functional significance of the pre-ERN that we observed on FAs, we computed additional analyses comparing ERP amplitudes for fast vs. slow hits. The average number of trials included in the ERP data was 38 (SD = 29, range 16–53) for fast hits, and 101 (SD = 30, range 11–63) for slow hits. We then tested whether mean ERP amplitudes to hits, commission errors, accuracy errors, fast hits and slow hits differed within the different time windows corresponding to the pre-ERN, ERN, Pe and FRN using a repeated-measures ANOVA, with the within-subject factors response type (commission error, accuracy error, fast hit, slow hit) and component (pre-ERN, ERN, Pe and FRN). A Greenhouse–Geisser correction was applied to control for nonsphericity in the data. Post-hoc Tukey tests were finally performed, with a significance threshold set to $p<.05$.

Source analysis

Source localization was performed using the Brain Electrical Source Analysis program (BESA®, Version 5.3). To control for differences due to other processes than cognitive control or error monitoring (e.g. unspecific visual or motor effects), source localization analysis was carried out on the error-minus-correct difference waveforms. This method allows to estimate inverse solutions for action monitoring potentials, when unwanted activities (i.e., the motor execution stage involving motor cortex regions and the feedback processing stage involving visual cortex regions) common to all conditions have been removed from the analysis and hence do not strongly bias the outcome in any direction (either motor or visual cortex; see Yeung et al., 2004; Vocat et al., 2008; Koban et al., 2010 for similar approaches). We used a standard four-shell ellipsoidal head model approximation (Scherg, 1990) registered to human brain atlas of Talairach & Tournoux (Talairach and Tournoux, 1988), that has already been used in previous error monitoring ERP studies (Dehaene et al., 1994; Herrmann et al., 2004; O'connell et al., 2007, 2009; Vocat et al., 2008). Similar to ERP mean amplitudes measures, we used time windows of −10 to +10 ms around each peak for dipole analysis. We first ran a principal component analysis of activity in each time window to estimate the minimum number of sources (objective criterion: ≥98% explained variance). We then used a generic algorithm to fit the dipoles, with no restriction to their direction or location.

Results

Behavior

On average, participants made 53% (SD = 6) hits with an average RT of 260 ms (SD = 38). The proportion of commission errors and accuracy errors was 20% (SD = 10) and 19% (SD = 8), respectively, a difference that did not reach statistical significance, $T(15) = .132$, $p = .886$. RTs for hits, for commission and accuracy errors as well as for hits preceding and following these three types of trials are shown in Fig. 3. Participants were significantly faster on commission errors (216 ms, SD = 37) compared to both hits and accuracy errors (263 ms, SD = 41), $Ts > 8.02$, $Ps < .001$, but there was no significant RT difference between hits and accuracy errors, $T = .926$, $p = .368$.

We found a significant post-error slowing (Rabbitt, 1966) after accuracy errors but not after commission errors. The RT was increased for hits following accuracy errors (266 ms, SD = 39) compared to hits following another hit (252 ms, SD = 40), $T = -3.02$, $p = .008$, and for hits following an accuracy error compared to hits following a commission error (250 ms, SD = 44), $T = 2.17$, $p = 0.046$. However, there was no significant RT difference for hits immediately following a commission error, as compared with hits that were immediately preceded by another hit, $T = .434$, $p = .67$.

Analysis of pre-error trials showed evidence for pre-error speeding before commission errors but not before accuracy errors. The RT was reduced for hits preceding a commission error (236 ms, SD = 43), as compared to hits preceding another hit (270 ms, SD = 39), $T = 6.17$, $p < .001$, and for hits preceding a commission error compared to hits preceding an accuracy error (270 ms, SD = 34), $T = 6.65$, $p < .001$. There was no difference in RT between

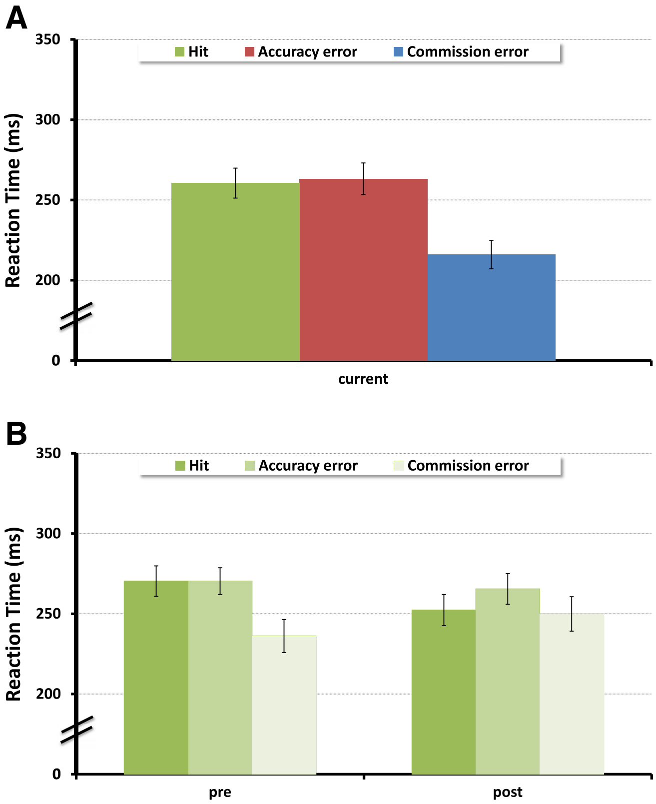


Fig. 3. RTs for hits, accuracy errors and commission errors on the current trial (A) and RTs for hits preceding (left) and following (right) another hit, an accuracy error or a commission error (B). Note. Error bars represent standard errors.

hits preceding an accuracy error and hits preceding another hit, $T = .006$, $p = .996$.

ERPs

ERP data from three participants who made in total 6 or less commission errors could not be included in the analyses (Olvet and Hajcak, 2009).[1] Response-locked ERPs are shown in Fig. 4 and error-minus-correct difference waveforms, topographic voltage maps and source localizations are shown in Fig. 5. ERP components and difference waveforms for fast and slow hits are also shown for comparison purposes.

Commission errors elicited several clear negative and positive deflections with maximal amplitude at FCz, preceding and following motor response: First, an initial negative component (average peak latency: 91 ms prior to response onset) consistent with the electrophysiological properties of the pre-ERN; then a second negative peak (average peak latency: 58 ms post response onset) followed by a more sustained positive component (average peak latency: 166 ms post response onset), corresponding to the ERN and Pe component, respectively. Accuracy errors were clearly associated with the generation of a delayed negative component (average peak latency: 227 ms post response onset) that we labeled FRN.

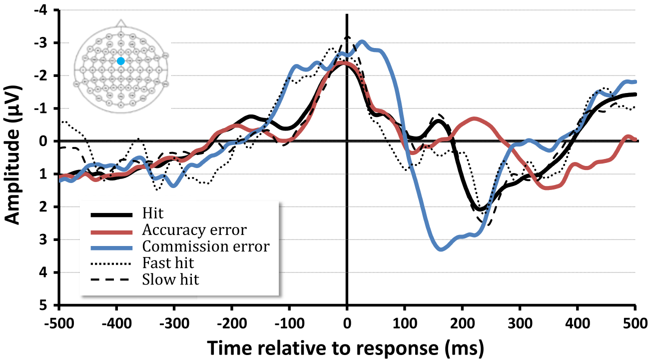


Fig. 4. Response-locked grand average ERPs at electrode FCz.

Mean amplitudes of the different ERP components in the different experimental conditions are summarized in Table 2. A multivariate repeated-measures ANOVA with response type (fast hit, slow hit, commission error, accuracy error) and component (pre-ERN, ERN, Pe and FRN) as factors disclosed significant main effects of component, $F(2.0,25.6) = 16.66$, $p < .001$, $\varepsilon = .66$, $\eta^2 = .56$, and of response type, $F(2.7,34.6) = 3.12$, $p = .043$, $\varepsilon = .89$, $\eta^2 = .19$, as well as a significant response type X component interaction, $F(4.1,53.1) = 16.18$, $p < .001$, $\varepsilon = .45$, $\eta^2 = .55$. Follow-up repeated-measures ANOVAs were carried out to further investigate the differential effects of response type on the amplitude of the ERP signal, separately for the pre-ERN, ERN, Pe and FRN. Effect of response type was significant for all four components, pre-ERN: $F(1.9,24.4) = 9.26$, $p < .001$, $\varepsilon = .62$, $\eta^2 = .43$; ERN: $F(1.6,20.5) = 9.10$, $p = .002$, $\varepsilon = .52$, $\eta^2 = .41$; Pe: $F(2.0,26.3) = 16.33$, $p < .001$, $\varepsilon = .67$, $\eta^2 = .56$ and FRN: $F(4,52) = 19.68$, $p < .001$, $\varepsilon = .75$, $\eta^2 = .60$.

Post-hoc Tukey tests confirmed that the pre-ERN was enhanced in amplitude for commission errors compared to accuracy errors, $p = .05$, and for fast hits compared to accuracy errors, $p = .01$, but there was no significant pre-ERN amplitude difference between commission errors and fast hits, and between accuracy errors and slow hits, all $Ps > .99$. The pre-ERN was also enhanced for fast hits compared to slow hits, $p = .04$, and there was a trend in the same direction for commission errors compared to slow hits, $p = 0.13$.

The ERN was larger in amplitude for commission errors compared to all other response types, all P's $< .02$, but none of the other pairwise comparisons reached statistical significance, all $Ps > .99$. Effects of response type on the Pe component were similar to those on the ERN component. The Pe had a larger amplitude for commission errors compared to all other response types, all $Ps < .004$ and there was no other significant difference, all $Ps > .46$.

Unlike the ERN and Pe, FRN amplitude was increased for accuracy errors in comparison to all three other response types, all $Ps < .03$. No other pairwise comparison was significant, all $Ps > .24$.

In sum, these results confirmed a dissociation between the monitoring of commission errors and accuracy errors. Whereas commission errors clearly elicited a pre-ERN, an ERN and a Pe component, accuracy errors elicited only a FRN component. These results also showed that fast hits also elicited a pre-ERN component, but no ERN, no Pe and no FRN component, suggesting that the pre-ERN may somehow be related to fast responding.

Because it occurred before the response (thus in the baseline period) and on trials with the fastest RT, we carried a series of control analysis on the pre-ERN, which aimed at better clarifying its actual functional significance (see Supplementary material S1). A potential problem arises from the possible component overlap of the pre-ERN with stimulus locked ERPs, including the P1 related to visual processing and the N2 related to conflict processing or inhibition (Botvinick, 2007; Folstein and Van Petten, 2008; van Veen and Carter, 2002). However, a direct influence of the NOGO N2

---

[1] We performed an additional analysis and removed the data of two participants who made only 8 commission errors. The new sample consisted of 14 participants with at least 12 trials included in an individual ERP average. Importantly, while on the one hand removing participants with low error count may yield better estimates of individual ERPs, on the other hand, this procedure also reduces the signal-to-noise-ratio of the grand average waveforms and the statistical power. It is noteworthy, however, that this new analysis yielded very similar ERP waveforms and statistical results. Thus, artificially increasing the number of error trials by removing subjects with low error rates did not change the main outcome of our study. In this paper, we therefore report the results obtained with these 16 participants.

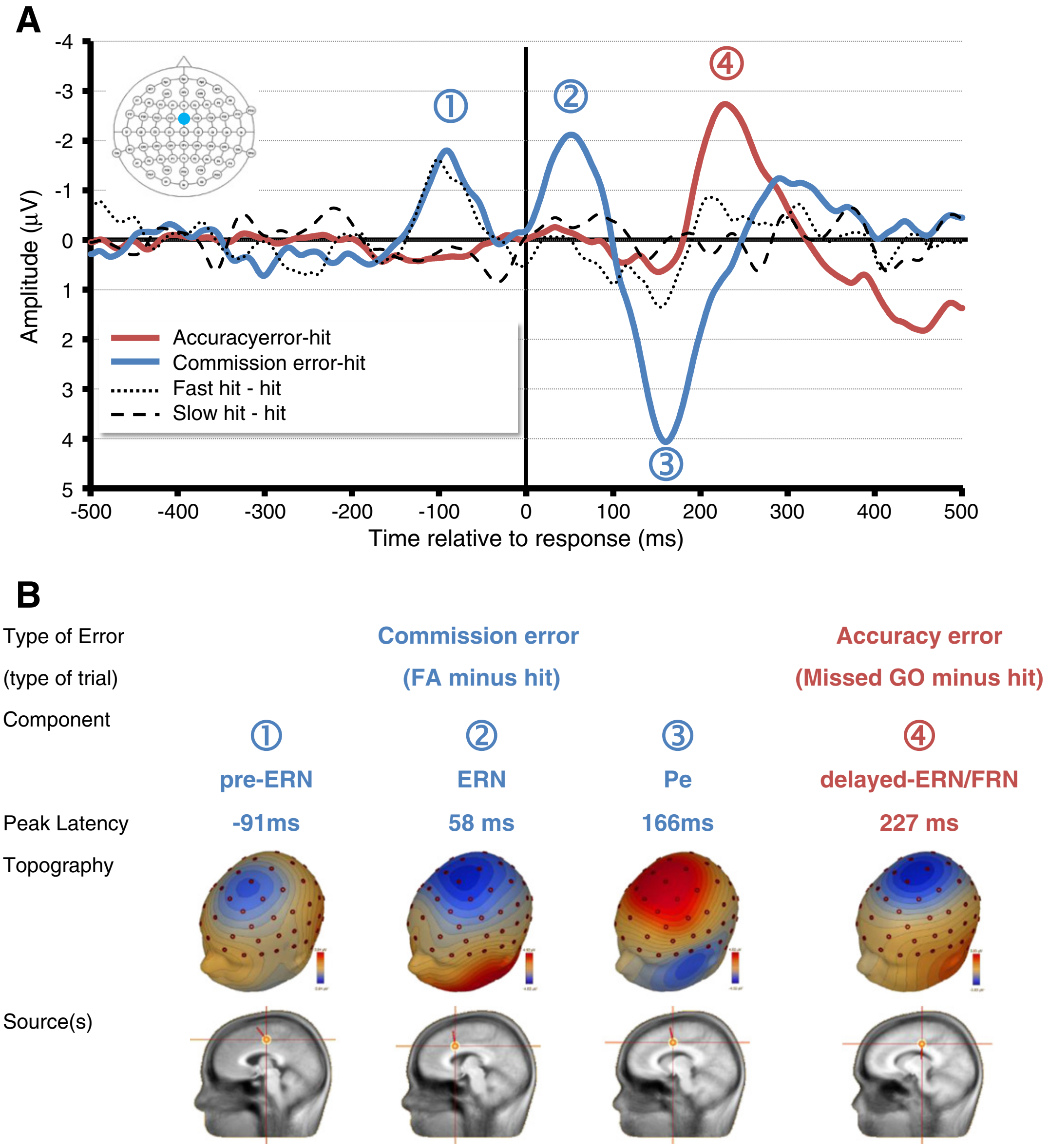


Fig. 5. Error-minus-correct difference ERP waveforms at electrode FCz (A); peak latency, scalp topographies and sources localization for each component (B).

component on the pre-ERN appears unlikely, for the following reasons: First, the latency of the pre-ERN component relative to stimulus onset was around 126 ms on average, which does not correspond to the mean latency of the N2 component, typically peaking 200 ms post-stimulus onset (Folstein and Van Petten, 2008). Second and more importantly, the N2 is usually observed on NOGO-, or high-conflict-trials, where enhanced cognitive control is required (Botvinick, 2007; Van Veen and Carter, 2002). In our results, the pre-ERN was observed not only for commission errors, but also for fast hits (thus following correct GO trials).

We performed additional control analyses to ascertain that the pre-ERN component was not accounted for by a component overlap, including the stimulus-locked P1. First, we performed a control analysis of response-locked ERPs using a pre-stimulus (instead of pre-response) baseline interval (see Fig. S1 from supplementary material). This analysis yielded similar results: the pre-ERN was significantly larger for commission errors relative to both hits and accuracy errors, suggesting that the pre-ERN is not simply a result of the use of a standard pre-response baseline to correct response-locked ERP waveforms.

Second, to explore the potential contribution of stimulus-locked ERP components to the pre-ERN, we analyzed and compared stimulus-locked ERPs at electrodes FCz and Oz (Figs. S2 and S3 in supplementary material). This control analysis showed that the pre-ERN was larger over frontal than occipital electrodes, and also larger for commission errors compared to the other experimental conditions. Although this result alone does not allow us to rule out a possible contribution of the stimulus-locked P1 in the generation of the pre-ERN, it suggests nonetheless that medial frontal (but not occipital) regions were likely involved in this process, consistent with the implication of action or error-monitoring brain structures. Remarkably, complementing source localization analysis of the pre-ERN (see p.16) corroborated this conclusion.

Table 2
Mean (SD) amplitudes of ERP components in the different conditions.

	Commission error	Accuracy error	Fast hit	Slow hit
Pre-ERN	0.25 (1.62)	−1.78 (2.08)	−1.84 (2.09)	−0.24 (1.28)
ERN	−0.5 (2.09)	−2.79 (2.01)	−0.39 (2.17)	−0.8 (1.67)
Pe	0.54 (3.02)	2.83 (1.99)	0.41 (2.09)	−0.73 (1.77)
FRN	−0.78 (2.13)	3.94 (3.35)	1.69 (1.54)	2.29 (1.99)

Third, in order to bring additional evidence for the involvement of the pre-ERN in anticipated responding, we divided hits (i.e., correctly aimed GO trials within the time limit) into four bins based on individuals' speed/RT and examined the impact of this variable on the amplitude of the pre-ERN component (see Figs. S4 and S5 in supplementary material). Repeated measures ANOVAs revealed that speed had a significant (linear) effect on the amplitude of the pre-ERN at FCz (i.e., larger pre-ERN for fast compared to slow RTs), but not at Oz, which is consistent with the interpretation that this pre-response component is somehow related to the monitoring of error likelihood based on the perceived speed (i.e., error likelihood presumably increases when RTs decrease). The lack of any significant amplitude modulation of the pre-ERN at electrode Oz by RT further suggests that this effect likely originated from frontal or central/cingulate brain regions (most likely performance monitoring processes within the medial frontal cortex/rostral cingulate zone or RCZ, as our source localization results confirmed, see here below), but did not merely index differential stimulus processing across conditions (commission errors vs. accuracy errors).

Fourth, to further examine whether a differential overlap between stimulus-locked and response-locked activities (due to RT differences between conditions) alone could account for the pre-ERN findings, we ran another control analysis on response-locked ERPs for the three conditions of interest (commission errors, accuracy errors and hits), computed for a subset of trials carefully matched in RT (Fig. S6 in supplementary material). This control analysis confirmed that the pre-ERN component was still visible (though slightly reduced) for commission errors in comparison to hits, when RTs were matched between conditions (hence when neutralizing potential stimulus-locked ERP effects), making it unlikely that the pre-ERN was mainly driven by a differential component overlap across conditions. Altogether, the results of these extensive control analyses suggest that this pre-response ERP component likely reflects error likelihood, being larger for risky (i.e., fast) decisions relative to safer (i.e., slower) perceptual decisions (see also Ruiz et al., 2009).

Finally, we performed an additional correlation analysis to assess whether the amplitude of the FRN might correlate with the magnitude of accuracy errors. For each participant separately, we calculated an average deviation (along the horizontal-x and vertical-y axis) between the position of the target on the screen and the actual position of the gunshot. We then calculated a between-subject rank-order Spearman correlation between this deviation (sum of the deviations on x and y axes) and the amplitude of the FRN generated for accuracy errors. This analysis showed that across participants, the amplitude of the FRN was significantly correlated with this average deviation ($r = -.57$, $p = .02$), indicated by a larger FRN component in participants with larger mean deviations.

Source analysis

Source localization results showed that a single source in the ACC ($x = 3.6$; $y = -14.4$; $z = 43.9$) accounted for more than 88% of the variance of the pre-ERN component (Fig. 5). A model with two non-overlapping generators accounted for more than 90% of the variance of the pre-ERN. One of these dipoles fell in the ACC ($x = 5.4$; $y = -1.3$; $z = 45.8$) and the other in the right superior temporal gyrus ($x = -70.2$; $y = -44.4$; $z = 7.6$). A model with two non-overlapping generators accounted for more than 90% of the variance of the ERN (Fig. 5). One of these dipoles fell in the ACC ($x = -9.4$; $y = -2.2$; $z = 39.4$) and the other in the right inferior temporal gyrus ($x = 53.4$; $y = -29.4$; $z = -17.1$). A single source in the ACC ($x = -3.8$; $y = 6.2$; $z = 37.0$) accounted for more than 94% of the variance of the Pe (Fig. 5). Finally, a single source in the ACC ($x = -11.4$; $y = -19.5$; $z = 37.3$) alike accounted for more than 90% of the variance of the FRN component (Fig. 5).

Discussion

The goal of this study was to compare the electrophysiological correlates of commission vs. accuracy errors in the same participants during a newly developed spatial GO-NOGO aiming task providing increased ecological validity. Participants made false alarms (i.e., commission errors) or performed gunshots that turned out to be spatially inaccurate relative to the position of the target (i.e., accuracy errors). Hence, the asset of this new "Shoot-NoShoot" paradigm is that the neural processing of these two types of errors could directly be compared using EEG measurements.

Using this new task, we show that commission and accuracy errors differ on various dimensions: First, behavioral results show the classical phenomenon of either pre-error speeding or post-error slowing, depending on the error type (Allain et al., 2009; Danielmeier and Ullsperger, 2011; Rabbitt, 1966). Commission errors were associated with pre-error speeding selectively, while post-error slowing was found for accuracy errors only. This dissociation confirmed that these two error types likely have different causes and consequences. Commission errors are probably caused by reduced cognitive or attentional control, and the consequent failure to inhibit a prepotent response (Britz and Michel, 2010; Pourtois, 2011). The use of an individually calibrated and adaptive response deadline as well as of a payoff schedule emphasizing both speed and accuracy may have exacerbated this speeding effect, and in turn the generation of a pre-ERN component, as we discuss below. Interestingly, the observation that accuracy errors, but not commission errors, led to a systematic post-error slowing suggests that these errors have different consequences for attention orienting (Notebaert et al., 2009) and/or cognitive control mechanisms (Botvinick et al., 2001). However, the fact that post-error slowing is often observed following commission errors in STOP tasks and GO/NOGO tasks (i.e., leading to inhibition failures), whereas pre-error speeding is typically found for interference tasks producing choice errors (Simon, Stroop or Flanker tasks), suggests that the dissociation found here between the two types of errors may actually be limited to the current paradigm. Future studies are needed to establish whether a similar dissociation can be evidenced using other tasks, which can also provide a direct comparison of different error types using a within-subject design, as in the present case.

The second major difference between these two error types was found at the electrophysiological level. Commission errors elicited a clear ERN/Pe complex immediately following response onset, with typical frontocentral topography and putative sources in the dACC, replicating previous ERP results (Dehaene et al., 1994; Falkenstein et al., 1991; Gehring et al., 1993; van Veen and Carter, 2006; Yeung et al., 2004). Unlike commission errors, accuracy errors were associated with the generation of a much later frontocentral negativity around 230 ms, which shared many electrophysiological properties with the FRN component, as previously described in the literature (Gehring and Willoughby, 2002; Hajcak et al., 2005; Miltner et al., 1997; Nieuwenhuis et al., 2004a, 2004b; Staedtgen et al., 2000). In our task, participants were shown the actual location on the screen of the aiming position, immediately after they pulled the trigger. This visual "feedback", synchronized with the motor response (i.e., release of the gun's trigger), timely informed them about the accuracy of their gunshot and thereby (indirectly) on the (spatial) discrepancy of their response. Contrary to commission errors (which can be assimilated to errors of choice, see Falkenstein et al., 2000), where the decision itself was erroneous and detected as such presumably on the basis of an internal motor representation, accuracy errors resulted from a correct decision, but the actual action execution turned out to be worse than expected, requiring extra processing time to detect these errors. We surmise that if accuracy errors would correspond to errors of choice, then their neural correlates and electrophysiological time-course would have been more comparable to commission errors, in line with the predictions of Falkenstein et al. (2000). However, another remarkable difference between the two error types is the absence of a Pe component for accuracy errors, relative to commission errors, such that even if accuracy errors would result from erroneous choices, it is striking that no Pe component was nevertheless generated in this condition. In this condition, participants could presumably not rely on an internal motor representation only, but instead, they had to rapidly process the visual feedback information in such a way to infer whether their gunshot was successful or not. This observation is consistent with the first indicator hypothesis of the RL theory (Holroyd and Coles, 2002; Nieuwenhuis et al., 2004a, 2004b), showing that rapid activation of a prediction error signal depends upon the type of errors made by the participants. Because commission errors can be detected on a first indicator made readily accessible through the internal monitoring of motor representations, the detection of accuracy errors is likely based on the rapid monitoring of external feedback information (Gentsch et al., 2009; Heldmann et al., 2008; Vocat et al., 2011). The selectivity of a Pe effect for commission errors might also hint at differences in error evaluation, and in subsequent adjustments in cognitive control, which might be more needed following failures of response inhibition (i.e., Commission errors).

The third difference between commission and accuracy errors is their absolute vs. relative nature: commission errors are qualitatively wrong decisions, whereas accuracy errors are relative, depending on the amount of deviation. Our results show that the neural mechanisms underlying error detection are not only sensitive to the occurrence of an error, but they might also be sensitive to the magnitude of these failures: The amplitude of the FRN following accuracy errors correlated negatively with the spatial discrepancy between the target and the actual location of the gunshot across subjects. This suggests that participants who were less accurate showed a larger FRN to accuracy errors, an observation that is consistent with the idea that this ERP component is modulated by the magnitude of (spatial) errors. Bernstein et al. (1995) already provided evidence for a parametric scaling of the amplitude of the ERN with the degree of error (see also Vocat et al., 2011). To the best of our knowledge, our study provides however the first evidence for a similar modulation of the FRN (hence not the ERN) with individual differences in spatial error magnitude. However, because our design only allowed us to compute this correlation across and not within subjects, further studies are needed to determine whether the FRN is also modulated in a similar way within subjects (across trials), and hence parametrically encodes the perceived severity of errors. Such a quantitative coding of the magnitude of an error would be consistent with a fine-tuned prediction error coding system (Fiorillo et al., 2003; Potts et al., 2010; Yasuda et al., 2004) and may depend on flexible reinforcement learning brain mechanisms (Holroyd et al., 2002; Nieuwenhuis et al., 2004a).

Another difference between commission errors and accuracy errors concerned the pre-ERN component, a frontocentral negativity occurring about 90 ms *prior* to the response and reflecting activity of the ACC as well, although being specific to commission errors. Because the pre-ERN preceded the response (and thus occurred during the pre-response baseline period) and was found only for trials with the fastest RTs, we conducted a series of additional control ERP analyzes on these data in order to clarify the functional meaning of this (premotor) component (see Supplementary material S1). These analyses included (i) response-locked ERPs computed with a pre-stimulus (instead of pre-response) baseline, (ii) stimulus-locked ERPs, (iii) response-locked ERPs for hits binned into 4 categories according to individual speed/RT, and (iv) response-locked ERPs for a subset of accuracy errors and hits that were carefully matched in speed (RT) with commission errors. Overall, these additional control analyses did not challenge our main interpretation that the pre-ERN reflects increased error-likelihood due to anticipated responding. They further suggest that (i) the pre-ERN component is not an artifact of the pre-response baseline, and that (ii) even though stimulus-locked activities may contribute to the pre-ERN (in line with our source localization results), differences in stimulus processing alone cannot account entirely for the amplitude variations found at the level of the pre-ERN component. (iii) Consistent with this view, we found a significant linear increase in pre-ERN amplitude with decreasing RT at FCz but not at Oz. This was further confirmed by our analysis of RT matched trials which also showed a significant (though reduced) pre-ERN component for commission errors compared to hits. Overall, these auxiliary analyses lent support to the notion that the pre-ERN is somehow related to the monitoring of error likelihood based on the perceived speed (i.e., error likelihood presumably increases when RTs decrease). Finally, despite a systematic and stable delay (mean = 13 ms, SD = 4) in the recording of the response by the light-gun shooting device by the EEG system (see Supplementary material S1), it appears improbable that pre-ERN solely results from any jitter in the recording of the response.

A similar pre-response ERN has been described previously by Ruiz and colleagues (2009). These authors recorded ERPs in expert pianists while they played memorized music pieces at a fast tempo in presence vs. absence of auditory feedback. They found a frontocentral negativity 70 ms prior to response errors (i.e., hitting the wrong key on the piano), with underlying cortical sources in the ACC, and interpreted this component as indicating an error signal of the self-monitoring system (Ruiz et al., 2009). In our spatial GO/NO-GO aiming task, the pre-ERN might reflect the detection of a fast, risky and thus potentially erroneous intention to shoot, and the associated increase in error likelihood (Brown and Braver, 2007). This increased error likelihood could result from reduced cognitive or attentional control due to anticipated and very fast responding, for example if the decision to shoot was made before enough perceptual evidence had accumulated. The ventral striatum and orbitofrontal cortex convey important evaluative signals about upcoming events, such as the expected reward and risk (Preuschoff et al., 2006; Schultz et al., 2008). Accordingly, interactions between the ACC and these additional structures could be involved in the generation of the pre-ERN, although further imaging work is needed to corroborate this prediction.

Further evidence that the pre-ERN reflects enhanced risk-related error likelihood is brought by the finding that fast hits also elicited a reliable pre-ERN, though no ERN, because these trials are associated with increased error likelihood but no error commission. Previous research already suggested a role for the ERN, and more generally the dACC, in error likelihood prediction (Brown and Braver, 2005; Potts et al., 2010) and risk prediction (Brown and Braver, 2007) as well as risk taking (Hewig et al., 2007, 2009; Polezzi et al., 2009; Yu and Zhou, 2009), but see Nieuwenhuis et al. (2007), Aarts et al. (2008), and Yeung and Nieuwenhuis (2009), for opposite evidence regarding this error-likelihood hypothesis. In these studies, risk is generally defined as an increased likelihood to obtain a negative compared to positive outcome. This applies to both utilitarian outcomes (e.g., negative reward in gambling tasks) and performance outcomes (e.g., erroneous responses and feedbacks). Our ERP results suggest that this notion could be extended to action monitoring effects taking place before the onset of the response, e.g. at the level of the pre-ERN.

In our study, error-likelihood or risk may arise from a conflict between (imperfect) stimulus processing and (premature) action preparation, which may result in anticipated responding (i.e., response preparation despite incomplete information processing). The finding that the pre-ERN is caused by anticipated responding (and the ERN by commission errors) is thus consistent with an interpretation of these components in terms of conflict-monitoring. In this framework, both a pre-ERN and ERN component are generated for NOGO trials because of fast/anticipated responding (probably due to incomplete stimulus processing) and post-action error detection mechanisms, respectively. Likewise, fast hits on GO trials are associated with a pre-

ERN component (i.e., anticipated responding) but no ERN because the actual outcome of the action can still be evaluated as either a hit or a miss (or a RT error). This post-action evaluation process necessarily relies on additional processing of the visual feedback that was shown almost simultaneously with the response. In case of inaccurate actions on GO trials (i.e., mislocalized shooting), an FRN was thus generated. However, further research is needed to examine whether the pre-ERN reflects the risky intention itself (conflict between stimulus processing and response), or the perceived increase in error likelihood and/or error anticipation following an uncertain intention.

Despite these differences in behavioral effects and electrophysiological correlates of commission vs. accuracy errors, our new EEG results also point at likely converging processing of these two different error types, as well as for the pre-response detection of increased error likelihood (see pre-ERN results). In line with most previous studies using dipole or distributed source localization approaches (e.g. Dhar et al., 2011; Gehring and Willoughby, 2002; Gehring et al., 1993; Herrmann et al., 2004; Koban et al., 2010; Vocat et al., 2008), we found sources in the dACC for the pre-ERN, the ERN, Pe, and the FRN component, supporting claims that these different components may all reflect shared reward prediction error signals (Holroyd and Coles, 2002) or alternatively, conflict detection mechanisms (Botvinick, 2007; Botvinick et al., 2001). However, it is also plausible that they reflect the contribution of dACC within distinct functional networks activated at non-overlapping latencies before and following motor response (Mathalon et al., 2003). Given that the dACC has massive reciprocal connections with cognitive, affective and motor systems, both at the cortical and subcortical levels (Margulies et al., 2007; Vogt et al., 1995), several neural circuits may contribute differentially to these error-related activities primarily generated within the dACC. In particular, the (post-response) ERN and the FRN are thought to reflect activity of a performance monitoring system comprising the dorsal ACC and the amygdala (Pourtois et al., 2010), as well as motor system (Yordanova et al., 2004). In the case of the ERN, the dACC may rely mainly on inputs from systems involved in motor preparation and representation, whereas the FRN may be associated with greater connectivity of the dACC with sensory systems conveying the external information used for outcome evaluation. By contrast, if the pre-ERN reflects an evaluation of error likelihood or risk taking, it is likely to be generated in a neural circuit comprising the pre-SMA, orbitofrontal cortex, ventral striatum and insula, where expectations and intentions are generated (Haynes et al., 2007; Lau et al., 2004; Preuschoff et al., 2008; Rushworth, 2008; Walton et al., 2004). Finally, the Pe component might reflect the activation of the dACC operating in concert with the insula, in such a way to enable the rapid conscious detection of response errors based on bodily or interoceptive signals (Dhar et al., 2011; Ullsperger et al., 2010). Future studies could use functional connectivity analyses of high density EEG and functional MRI data to assess what are the different inputs to dACC which contribute to eliciting similar prediction error signals at distinct processing stages during action and error monitoring.

Although the localization of these sources may appear slightly more posterior compared to previous fMRI or animal studies, these inverse solutions were actually very similar (cf. RCZ) to those reported in previous EEG studies which used GO-NOGO tasks, the same head model and the same source localization algorithm (Koban et al., 2010; Vocat et al., 2008, 2011). Moreover, this region of the posterior medial frontal cortex (as evidenced with our source localization method) is also usually found in previous imaging studies focused on performance monitoring brain processes (Klein et al., 2007). However, some caution is needed when interpreting the present source localization results, based on dipole modeling. This method was primarily used as an indirect confirmatory analysis for the likely involvement of generic error monitoring brain systems involving the medial frontal cortex/RCZ in our study, whose latency mainly depends on the type of error being made. More generally, these source localization results appear consistent with earlier reports on error monitoring brain processes based on grand-average ERP data, as opposed to difference waveforms (e.g., Dhar et al., 2011; Herrmann et al., 2004).

To the best of our knowledge, our study is the first to investigate error monitoring using a novel light-gun response device, which provides enhanced ecological validity and kept the experiment engaging for participants. Moreover, our Shoot/NoShoot paradigm enabled a within-subject comparison between two different types of response errors, commission and accuracy errors, with different electrophysiological responses. Our ERP results show a clear dissociation between the two types of errors. Commission errors, result from an erroneous decision likely due to anticipated responding and elicited a pre-ERN, an ERN and a Pe time-locked to the response. Conversely, accuracy errors likely result from an incorrect action, elicited a FRN following response feedback (i.e., not following performance feedback) but no pre-ERN, ERN or Pe. Accordingly, these ERP components may thus reflect the activity of a generic error monitoring brain system in RCZ, which may generate a prediction error signal at different stages of action monitoring (e.g. planning and realization). As such, these new results bring a novel contribution to our understanding of brain processes involved in the swift detection of response errors or action failures, while being consistent with the dominant theoretical framework put forward in the cognitive neuroscience literature to account for our remarkable ability to exert control during action monitoring and eventually yield the rapid detection of unfavorable outcomes.

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2012.02.010.

Acknowledgments

This research was supported by the Swiss National Centre of Competence in Research in the Affective Sciences, project N° 51NF40-128911. GP is funded by the European Research Council (Starting Grant #200758) and Ghent University (BOF Grant #05Z01708).

The authors thank Dr. Yann Cojan and other members of the Social Error and Conflict Society (SECS), for their useful comments on an earlier version of this manuscript.

References

Aarts, E., Roelofs, A., Van Turennout, M., 2008. Anticipatory activity in anterior cingulate cortex can be independent of conflict and error likelihood. J. Neurosci. 28, 4671–4678.

Allain, S., Burle, B., Hasbroucq, T., Vidal, F., 2009. Sequential adjustments before and after partial errors. Psychon. Bull. Rev. 16, 356–362.

Bernstein, P.S., Scheffers, M.K., Coles, M.G., 1995. "Where did I go wrong?" A psychophysiological analysis of error detection. J. Exp. Psychol. Hum. Percept. Perform. 21, 1312–1322.

Botvinick, M.M., 2007. Conflict monitoring and decision making: reconciling two perspectives on anterior cingulate function. Cogn. Affect. Behav. Neurosci. 7, 356–366.

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. Psychol. Rev. 108, 624–652.

Brazdil, M., Roman, R., Daniel, P., Rektor, I., 2005. Intracerebral error-related negativity in a simple Go/NoGo task. J. Psychophysiol. 19, 244–255.

Brazdil, M., Roman, R., Falkenstein, M., Daniel, P., Jurak, P., Rektor, I., 2002. Error processing—evidence from intracerebral ERP recordings. Exp. Brain Res. 146, 460–466.

Britz, J., Michel, C.M., 2010. Errors can be related to pre-stimulus differences in ERP topography and their concomitant sources. Neuroimage 49, 2774–2782.

Brown, J.W., Braver, T.S., 2005. Learned predictions of error likelihood in the anterior cingulate cortex. Science 307, 1118–1121.

Brown, J.W., Braver, T.S., 2007. Risk prediction and aversion by anterior cingulate cortex. Cogn. Affect. Behav. Neurosci. 7, 266–277.

Danielmeier, C., Ullsperger, M., 2011. Post-error adjustments. Front. Psychol. 2, 233.

Debener, S., Ullsperger, M., Siegel, M., Fiehler, K., Von Cramon, D.Y., Engel, A.K., 2005. Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. J. Neurosci. 25, 11730–11737.

Dehaene, S., Posner, M.I., Tucker, D.M., 1994. Localization of a neural system for error-detection and compensation. Psychol. Sci. 5, 303–305.

Dhar, M., Pourtois, G., 2011. Early error detection is generic, but subsequent adaptation to errors is not: evidence from ERPs. Neuropsychologia 49 (5), 1236–1245.

Dhar, M., Wiersema, J.R., Pourtois, G., 2011. Cascade of neural events leading from error commission to subsequent awareness revealed using EEG source imaging. PLoS One 6, e19578.

Eichele, H., Juvodden, H.T., Ullsperger, M., Eichele, T., 2010. Mal-adaptation of event-related EEG responses preceding performance errors. Front. Hum. Neurosci. 4.

Emeric, E.E., Brown, J.W., Leslie, M., Pouget, P., Stuphorn, V., Schall, J.D., 2008. Performance monitoring local field potentials in the medial frontal cortex of primates: anterior cingulate cortex. J. Neurophysiol. 99, 759–772.

Eppinger, B., Kray, J., Mock, B., Mecklinger, A., 2008. Better or worse than expected? Aging, learning, and the ERN. Neuropsychologia 46, 521–539.

Falkenstein, M., Hohnsbein, J., Hoormann, J., Blanke, L., 1991. Effects of crossmodal divided attention on late ERP components. II. Error processing in choice reaction tasks. Electroencephalogr. Clin. Neurophysiol. 78, 447–455.

Falkenstein, M., Hoormann, J., Christ, S., Hohnsbein, J., 2000. ERP components on reaction errors and their functional significance: a tutorial. Biol. Psychol. 51, 87–107.

Fiorillo, C.D., Tobler, P.N., Schultz, W., 2003. Discrete coding of reward probability and uncertainty by dopamine neurons. Science 299, 1898–1902.

Folstein, J.R., Van Petten, C., 2008. Influence of cognitive control and mismatch on the N2 component of the ERP: a review. Psychophysiology 45, 152–170.

Frank, M.J., Woroch, B.S., Curran, T., 2005. Error-related negativity predicts reinforcement learning and conflict biases. Neuron 47, 495–501.

Gehring, W.J., Goss, B., Coles, M.G.H., Meyer, D.E., Donchin, E., 1993. A neural system for error-detection and compensation. Psychol. Sci. 4, 385–390.

Gehring, W.J., Willoughby, A.R., 2002. The medial frontal cortex and the rapid processing of monetary gains and losses. Science 295, 2279–2282.

Gentsch, A., Ullsperger, P., Ullsperger, M., 2009. Dissociable medial frontal negativities from a common monitoring system for self- and externally caused failure of goal achievement. Neuroimage 47, 2023–2030.

Gratton, G., Coles, M.G., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468–484.

Hajcak, G., Holroyd, C.B., Moser, J.S., Simons, R.F., 2005. Brain potentials associated with expected and unexpected good and bad outcomes. Psychophysiology 42, 161–170.

Hajcak, G., Moser, J.S., Holroyd, C.B., Simons, R.F., 2006. The feedback-related negativity reflects the binary evaluation of good versus bad outcomes. Biol. Psychol. 71, 148–154.

Halgren, E., Boujon, C., Clarke, J., Wang, C., Chauvel, P., 2002. Rapid distributed fronto-parieto-occipital processing stages during working memory in humans. Cereb. Cortex 12, 710–728.

Haynes, J.D., Sakai, K., Rees, G., Gilbert, S., Frith, C., Passingham, R.E., 2007. Reading hidden intentions in the human brain. Curr. Biol. 17, 323–328.

Heldmann, M., Russeler, J., Munte, T.F., 2008. Internal and external information in error processing. BMC Neurosci. 9, 33.

Herrmann, M.J., Rommler, J., Ehlis, A.C., Heidrich, A., Fallgatter, A.J., 2004. Source localization (LORETA) of the error-related-negativity (ERN/Ne) and positivity (Pe). Brain Res. Cogn. Brain Res. 20, 294–299.

Hewig, J., Straube, T., Trippe, R.H., Kretschmer, N., Hecht, H., Coles, M.G.H., Miltner, W.H.R., 2009. Decision-making under risk: an fMRI study. J. Cogn. Neurosci. 21, 1642–1652.

Hewig, J., Trippe, R., Hecht, H., Coles, M.G., Holroyd, C.B., Miltner, W.H., 2007. Decision-making in blackjack: an electrophysiological analysis. Cereb. Cortex 17, 865–877.

Holroyd, C.B., Coles, M.G., 2002. The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. Psychol. Rev. 109, 679–709.

Holroyd, C.B., Coles, M.G., Nieuwenhuis, S., 2002. Medial prefrontal cortex and error potentials. Science 296, 1610–1611 (author reply 1610–1611).

Holroyd, C.B., Nieuwenhuis, S., Yeung, N., Nystrom, L., Mars, R.B., Coles, M.G., Cohen, J.D., 2004. Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. Nat. Neurosci. 7, 497–498.

Keil, J., Weisz, N., Paul-Jordanov, I., Wienbruch, C., 2010. Localization of the magnetic equivalent of the ERN and induced oscillatory brain activity. Neuroimage 51, 404–411.

Klein, T.A., Endrass, T., Kathmann, N., Neumann, J., Von Cramon, D.Y., Ullsperger, M., 2007. Neural correlates of error awareness. Neuroimage 34, 1774–1781.

Koban, L., Pourtois, G., Vocat, R., Vuilleumier, P., 2010. When your errors make me lose or win: event-related potentials to observed errors of cooperators and competitors. Soc. Neurosci. 5, 360–374.

Krigolson, O.E., Pierce, L.J., Holroyd, C.B., Tanaka, J.W., 2009. Learning to become an expert: reinforcement learning and the acquisition of perceptual expertise. J. Cogn. Neurosci. 21, 1834–1841.

Lau, H.C., Rogers, R.D., Ramnani, N., Passingham, R.E., 2004. Willed action and attention to the selection of action. Neuroimage 21, 1407–1415.

Luu, P., Tucker, D.M., Derryberry, D., Reed, M., Poulsen, C., 2003. Electrophysiological responses to errors and feedback in the process of action regulation. Psychol. Sci. 14, 47–53.

Margulies, D.S., Kelly, A.M., Uddin, L.Q., Biswal, B.B., Castellanos, F.X., Milham, M.P., 2007. Mapping the functional connectivity of anterior cingulate cortex. Neuroimage 37, 579–588.

Mathalon, D.H., Whitfield, S.L., Ford, J.M., 2003. Anatomy of an error: ERP and fMRI. Biol. Psychol. 64, 119–141.

Miltner, W.H., Lemke, U., Weiss, T., Holroyd, C., Scheffers, M.K., Coles, M.G., 2003. Implementation of error-processing in the human anterior cingulate cortex: a source analysis of the magnetic equivalent of the error-related negativity. Biol. Psychol. 64, 157–166.

Miltner, W.H.R., Braun, C.H., Coles, M.G.H., 1997. Event-related brain potentials following incorrect feedback in a time-estimation task: evidence for a “generic” neural system for error detection. J. Cogn. Neurosci. 9, 788–798.

Nieuwenhuis, S., Holroyd, C.B., Mol, N., Coles, M.G., 2004a. Reinforcement-related brain potentials from medial frontal cortex: origins and functional significance. Neurosci. Biobehav. Rev. 28, 441–448.

Nieuwenhuis, S., Ridderinkhof, K.R., Blom, J., Band, G.P., Kok, A., 2001. Error-related brain potentials are differentially related to awareness of response errors: evidence from an antisaccade task. Psychophysiology 38, 752–760.

Nieuwenhuis, S., Schweizer, T.S., Mars, R.B., Botvinick, M.M., Hajcak, G., 2007. Error-likelihood prediction in the medial frontal cortex: a critical evaluation. Cereb. Cortex 17, 1570–1581.

Nieuwenhuis, S., Yeung, N., Holroyd, C.B., Schurger, A., Cohen, J.D., 2004b. Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. Cereb. Cortex 14, 741–747.

Niki, H., Watanabe, M., 1979. Prefrontal and cingulate unit-activity during timing behavior in T T monkey. Brain Res. 171, 213–224.

Notebaert, W., Houtman, F., Opstal, F.V., Gevers, W., Fias, W., Verguts, T., 2009. Post-error slowing: an orienting account. Cognition 111, 275–279.

O'connell, R.G., Dockree, P.M., Bellgrove, M.A., Kelly, S.P., Hester, R., Garavan, H., Robertson, I.H., Foxe, J.J., 2007. The role of cingulate cortex in the detection of errors with and without awareness: a high-density electrical mapping study. Eur. J. Neurosci. 25, 2571–2579.

O'connell, R.G., Dockree, P.M., Bellgrove, M.A., Turin, A., Ward, S., Foxe, J.J., Robertson, I.H., 2009. Two types of action error: electrophysiological evidence for separable inhibitory and sustained attention neural mechanisms producing error on go/no-go tasks. J. Cogn. Neurosci. 21, 93–104.

Olvet, D.M., Hajcak, G., 2009. The stability of error-related brain activity with increasing trials. Psychophysiology 46, 957–961.

Overbeek, T.J.M., Nieuwenhuis, S., Ridderinkhof, K.R., 2005. Dissociable components of error processing — on the functional significance of the Pe Vis-a-vis the ERN/Ne. J. Psychophysiol. 19, 319–329.

Picton, T.W., Bentin, S., Berg, P., Donchin, E., Hillyard, S.A., Johnson Jr., R., Miller, G.A., Ritter, W., Ruchkin, D.S., Rugg, M.D., Taylor, M.J., 2000. Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. Psychophysiology 37, 127–152.

Polezzi, D., Sartori, G., Rumiati, R., Vidotto, G., Daum, I., 2009. Brain correlates of risky decision-making. Neuroimage.

Potts, G.F., Martin, L.E., Kamp, S.M., Donchin, E., 2010. Neural response to action and reward prediction errors: comparing the error-related negativity to behavioral errors and the feedback-related negativity to reward prediction violations. Psychophysiology.

Pourtois, G., 2011. Early error detection predicted by reduced pre-response control process: an ERP topographic mapping study. Brain Topogr. 23, 403–422.

Pourtois, G., Vocat, R., N'diaye, K., Spinelli, L., Seeck, M., Vuilleumier, P., 2010. Errors recruit both cognitive and emotional monitoring systems: simultaneous intracranial recordings in the dorsal anterior cingulate gyrus and amygdala combined with fMRI. Neuropsychologia 48, 1144–1159.

Preuschoff, K., Bossaerts, P., Quartz, S.R., 2006. Neural differentiation of expected reward and risk in human subcortical structures. Neuron 51, 381–390.

Preuschoff, K., Quartz, S.R., Bossaerts, P., 2008. Human insula activation reflects risk prediction errors as well as risk. J. Neurosci. 28, 2745–2752.

Rabbitt, P.M.A., 1966. Errors and error correction in choice-response tasks. J. Exp. Psychol. 71, 264.

Ridderinkhof, K.R., Nieuwenhuis, S., Bashore, T.R., 2003. Errors are foreshadowed in brain potentials associated with action monitoring in cingulate cortex in humans. Neurosci. Lett. 348, 1–4.

Ridderinkhof, K.R., Ramautar, J.R., Wijnen, J.G., 2009. To P(E) or not to P(E): a P3-like ERP component reflecting the processing of response errors. Psychophysiology 46, 531–538.

Ruiz, M.H., Jabusch, H.C., Altenmuller, E., 2009. Detecting wrong notes in advance: neuronal correlates of error monitoring in pianists. Cereb. Cortex 19, 2625–2639.

Rushworth, M.F., 2008. Intention, choice, and the medial frontal cortex. Ann. N. Y. Acad. Sci. 1124, 181–207.

Rushworth, M.F., Behrens, T.E., 2008. Choice, uncertainty and value in prefrontal and cingulate cortex. Nat. Neurosci. 11, 389–397.

San Martin, R., Manes, F., Hurtado, E., Isla, P., Ibanez, A., 2010. Size and probability of rewards modulate the feedback error-related negativity associated with wins but not losses in a monetarily rewarded gambling task. Neuroimage 51, 1194–1204.

Scherg, M., 1990. Fundamentals of dipole source potential analysis. In: Grandori, M.H.F., Romani, G.L. (Eds.), Auditory Evoked Magnetic Fields and Electric Potentials. Advances in Audiology. Karger, Basel, pp. 40–69.

Schultz, W., Preuschoff, K., Camerer, C., Hsu, M., Fiorillo, C.D., Tobler, P.N., Bossaerts, P., 2008. Explicit neural signals reflecting reward uncertainty. Philos. Trans. R. Soc. Lond. B Biol. Sci. 363, 3801–3811.

Shalgi, S., Barkan, I., Deouell, L.Y., 2009. On the positive side of error processing: error-awareness positivity revisited. Eur. J. Neurosci. 29, 1522–1532.

Staedtgen, M., Ruchsow, M., Kiefer, M., Spitzer, M., 2000. Error-related negativity evoked by internal error-detection and external feedback. J. Cogn. Neurosci. 114-114.

Stahl, J., 2010. Error detection and the use of internal and external error indicators: an investigation of the first-indicator hypothesis. Int. J. Psychophysiol. 77, 43–52.

Steinhauser, M., Yeung, N., 2010. Decision processes in human performance monitoring. J. Neurosci. 30, 15643–15653.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme, New York.

Ullsperger, M., Harsay, H.A., Wessel, J.R., Ridderinkhof, K.R., 2010. Conscious perception of errors and its relation to the anterior insula. Brain Struct. Funct. 214, 629–643.
Van Veen, V., Carter, C.S., 2002. The anterior cingulate as a conflict monitor: fMRI and ERP studies. Physiol. Behav. 77, 477–482.
Van Veen, V., Carter, C.S., 2006. Error detection, correction, and prevention in the brain: a brief review of data and theories. Clin. EEG Neurosci. 37, 330–335.
Vocat, R., Pourtois, G., Vuilleumier, P., 2008. Unavoidable errors: a spatio-temporal analysis of time-course and neural sources of evoked potentials associated with error processing in a speeded task. Neuropsychologia 46, 2545–2555.
Vocat, R., Pourtois, G., Vuilleumier, P., 2011. Parametric modulation of error-related ERP components by the magnitude of visuo-motor mismatch. Neuropsychologia 49, 360–367.
Vogt, B.A., Nimchinsky, E.A., Vogt, L.J., Hof, P.R., 1995. Human cingulate cortex: surface features, flat maps, and cytoarchitecture. J. Comp. Neurol. 359, 490–506.
Walton, M.E., Devlin, J.T., Rushworth, M.F., 2004. Interactions between decision making and performance monitoring within prefrontal cortex. Nat. Neurosci. 7, 1259–1265.
Wang, C.M., Ulbert, I., Schomer, D.L., Marinkovic, K., Halgren, E., 2005. Responses of human anterior cingulate cortex microdomains to error detection, conflict monitoring, stimulus–response mapping, familiarity, and orienting. J. Neurosci. 25, 604–613.
Yasuda, A., Sato, A., Miyawaki, K., Kumano, H., Kuboki, T., 2004. Error-related negativity reflects detection of negative reward prediction error. Neuroreport 15, 2561–2565.
Yeung, N., Cohen, J.D., Botvinick, M.M., 2004. The neural basis of error detection: conflict monitoring and the error-related negativity. Psychol. Rev. 111, 931–959.
Yeung, N., Nieuwenhuis, S., 2009. Dissociating response conflict and error likelihood in anterior cingulate cortex. J. Neurosci. 29, 14506–14510.
Yordanova, J., Falkenstein, M., Hohnsbein, J., Kolev, V., 2004. Parallel systems of error processing in the brain. Neuroimage 22, 590–602.
Yu, R., Zhou, X., 2006. Brain potentials associated with outcome expectation and outcome evaluation. Neuroreport 17, 1649–1653.
Yu, R., Zhou, X., 2009. To bet or not to bet? The error negativity or error-related negativity associated with risk-taking choices. J. Cogn. Neurosci. 21, 684–696.