Error-Related Brain Activity Reflects Independent Systems in Human Error Monitoring

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ABSTRACT

Performance monitoring is a key function of human cognition and critical for achieving goal-directed behavior. In recent years, research has particularly focused on how the brain detects and evaluates behavioral errors. Most studies investigated two neural correlates of performance monitoring in the human scalp EEG. In particular, the error-related negativity (Ne/ERN) is a negative fronto-central deflection observed immediately after an erroneous response, representing an early and unconscious stage of error processing. The Ne/ERN is followed by the later error positivity (Pe), a broader positivity viewed as a correlate of conscious error processing. Whereas a large amount of research has been conducted on these neural correlates, fundamental questions on their relationship remain. Crucially, it is still unclear whether both components represent functionally independent processes of error monitoring or whether the two components are part of a single mechanism. The first possibility implies that the earlier Ne/ERN provides the basis for the later emergence of the Pe and error awareness in a cascade-like architecture of error monitoring. The other possibility is that the Pe and error awareness can emerge independently of the Ne/ERN, which implies that different error monitoring mechanisms exist and may proceed independently. The thesis addresses the important question whether Ne/ERN provides necessary information for error awareness and Pe. To this aim, behavioral and psychophysiological studies were conducted:

(1) In a first part, we investigated whether Ne/ERN and Pe are causally related (study 1). We developed a novel experimental paradigm based on the classical

letters flanker task. In this paradigm, participants have to classify targets but ignore irrelevant distractors (flankers) that are always associated with an incorrect response. Targets but not flankers are masked with varying target-masking intervals. On some trials, no target at all is presented, thus preventing the representation of a correct response. Importantly, the lack of a representation of the correct response also prevents the emergence of Ne/ERN. However, because flankers are easily visible and responses to these flankers are always incorrect, conscious detection of these flanker errors is still possible. The presence of a Pe in the absence of Ne/ERN for flanker errors provides evidence for independent error monitoring processes.

(2) In a second part, we investigated whether the Ne/ERN and Pe are differentially sensitive to temporal aspects of conscious error detection. Whereas the Pe is assumed to be the earliest correlate of the emergence of conscious error perception, participants often report the feeling of having detected an error even before the erroneous response was actually executed ("early error sensations"). The first goal of this part was to investigate whether such anecdotal evidence can be measured empirically. In study 2, a series of behavioral experiments using different methodological procedures were conducted. Participants during choice tasks have to report whether errors were accompanied or not by early error sensations (i.e. early and late detected errors) or give confidence judgments about early error sensations. Participants frequently reported early errors with high level of confidence. Subsequently, we studied how error-related brain activity reflects the emergence of early error sensations. In study 3, we measured EEG activity and compared early and late detected errors. Results showed that while the Pe reliably reflects the early error sensations (larger amplitude for early errors), the Ne/ERN does not (no

differences between early and late errors). Crucially, the Ne/ERN and the Pe responded differently to temporal aspects of error awareness, meaning that Ne/ERN and Pe could rely on different types of information for error detection. This again speaks for the idea of independent systems of error monitoring.

CONTENTS

OVERVIEW

Human behavior is error prone (Reason, 1990) and consequences of these errors can be fatal. For instance, in public transportation, many human lives may depend on the performance of a single driver. Therefore, monitoring one's own action outcomes and adjusting behavior to optimize performance are of fundamental importance.

Years of research evidenced a system in the brain to monitor our performance, which enables goal-directed behavior. This system monitors and detects task-goal violations as behavioral errors and adjusts performance accordingly. Neural activity within the medial frontal cortex has been found to support these functions (Carter et al., 1998; Matsumoto, Matsumoto, Abe, & Tanaka, 2007; Rushworth, Walton, Kennerley, & Bannerman, 2004). This performance monitoring signals the need for increased control, whenever task-goals are not achieved or the risk to fail is high (Kerns et al., 2004; Ridderinkhof, Van Den Wildenberg, Segalowitz, & Carter, 2004). A neural signature for error detection is the error negativity (Ne) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991) or error-related negativity (ERN) (Gehring, Goss, Coles, Meyer, & Donchin, 1993) a negative deflection in the response-locked ERPs presumably generated in the medial frontal cortex (Dehaene, Posner, & Tucker, 1994). The Ne/ERN emerges in an early stage of error processing (around erroneous response execution) as an automatic and unconscious error detection signal (S Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). The Ne/ERN is followed by a broader posterior error positivity (Pe) emerging in a later stage of error processing, approximately 300 milliseconds after the execution of an erroneous response (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). The Pe is often considered a correlate of error awareness. In particular, the Pe is supposed to reflect the accumulated sensory, motor and cognitive evidence, which creates the conscious representation of errors (Wessel, Danielmeier, & Ullsperger, 2011). One important and still open question concerns the relation between Ne/ERN and Pe and between early and late stages of error processing. Indeed, there is an ongoing debate on the question whether the Ne/ERN is necessary to create conscious representations of errors. Evidence of a necessary contribution of Ne/ERN for error awareness would imply a cascade-like architecture of the performance monitoring system where the Ne/ERN forms the basis for the Pe and for error awareness (Dhar, Wiersema, & Pourtois, 2011; Wessel et al., 2011). Alternatively, the Ne/ERN can be part of an independent system, which does not provide necessary information for conscious error awareness. Importantly, investigating the neural basis of error processing could be a valuable method for understanding how the performance monitoring system processes errors to achieve conscious error awareness.

Overall, the central aim of this thesis is to study the architecture of the performance monitoring system and the interaction between early signals of performance monitoring and later conscious error perception. More specifically, I aim to address the question whether the early Ne/ERN provides necessary information for the emergence of conscious error detection and for the emergence of later correlates of error awareness (i.e. the Pe). Methodologically, EEG and behavioral measures are collected to study the performance monitoring system during error processing.

To address the questions about the relation between correlates of performance monitoring, it is necessary to first specify the role of the performance monitoring system in cognitive control and the mechanisms of conscious perception. Thus, in the first part of the present thesis, the most important theoretical and methodological considerations on performance monitoring, cognitive control and conscious perception are introduced. Then, I will focus specifically on the EEG correlates of the performance monitoring system during error processing. Finally, three studies with behavioral and EEG data are exposed and the architecture of the performance monitoring system and of conscious error perception is discussed.

In the next paragraphs, the role of the performance monitoring system in cognitive control is introduced. Further, an overview on philosophical and neuroscientific theories of consciousness will be provided.

INTRODUCTION

The performance monitoring system and cognitive control

Cognitive control can be defined as sets of high-level processes that organize, regulate and coordinate mental operations. These processes can operate during extended periods of time to make a decision to act (Norman & Shallice, 1986). Cognitive control can be implemented in those situations where routine behaviors are inadequate or when pre-established action patterns are not present. These situations include: planning, problem solving, reasoning and complex decision-making.

A fundamental question is how the brain knows when to implement cognitive control, and when to simply allow pre-established stimulus–response (S–R) associations to be executed. For this reason, cognitive control requires a system to monitor ongoing performance. Such a system can implement cognitive control whenever it is necessary in order to select thoughts or actions in relation to internal goals (Kouneiher, Charron, & Koechlin, 2009). Indeed, the organization of behavior and cognition into coordinated and goal-directed actions is arguably the essence of cognitive control (Matsumoto, Suzuki, & Tanaka, 2003; Matsumoto & Tanaka, 2004). From this perspective, performance monitoring allows detection of behavioral errors and of task goal violations. Through error detection it is possible to determine when additional control is required, and in turn, enable an increase of cognitive control signals to regulate and coordinate behavior (Badre, Hoffman, Cooney, & D'Esposito, 2009). To this aim, the performance monitoring system can accumulate error-related evidence, based on information processing, and initiate the appropriate corrections to avoid errors in the future. For instance, after errors, the performance monitoring can initiate post-error behavioral adjustments, like slowing down after error commission (Rabbitt, 1966).

The performance monitoring system can monitor different types of information for error detection and can allow external (based on actions, behaviors and outcomes) and internal monitoring (based on cognitive, emotional and visceral states). Thus, task goal violations, negative outcome, conflict between incompatible stimuli or responses and emotional relevant stimuli represent some of the crucial monitored information to signal the need for increasing control (Cohen, Botvinick, & Carter, 2000).

The Eriksen Flanker task (Eriksen & Eriksen, 1974) is a task frequently used to study performance monitoring. In this task, stimuli can be strings of oriented arrowheads (e.g. <<><<). The task goal is to respond to the central target stimulus while ignoring the lateral distractor stimuli, the flankers. Flanker stimuli can have either the same orientation as the target (congruent condition <<<<<) or a different orientation (incongruent condition <<><<). Crucially, on incongruent trials, the stimulus activates both the correct and the erroneous responses and therefore, a higher level of cognitive conflict between mutually exclusive response alternatives arises. In this context of high cognitive conflict, the risk to commit errors (i.e. a response to the flanker and not to the target) is high. The activity of medial prefrontal cortex (mPFC) has been proposed to detect the level of conflict and to be a signal of error detection (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter et al., 1998; Dehaene et al., 1994; Yeung, Botvinick, & Cohen, 2004). Based on this evidence, areas of the mPFC, as the anterior cingulate cortex (ACC), are considered parts of the neural substrates of a human performance monitoring system (Carter et al., 1998; Dehaene et al., 1994; Sheth et al., 2012; Swick & Turken, 2002).

Arguably, fast error detection and conscious error perception are important elements to implement cognitive control. Importantly, a complete and accurate representation of an error can contribute to flexible adjustments and adaptive goal-directed behavior (Maier, Yeung, & Steinhauser, 2011). However, the mechanisms of error detection and compensation and how conscious error perception is achieved in the brain are still matter of debate. Moreover, studying conscious error perception implicates methodological and theoretical considerations that need to be addressed. Thus, in the next part, some concepts and theories on conscious perception will be introduced.

Consciousness and metacognition

The problem of consciousness includes several questions: How do brain processes interact to create conscious mental representations? What brain processes underlie mental representations and our capacity to be conscious of a specific piece of information? How can a physical system achieve conscious awareness about external stimuli and internal states? What is the relation between the mind and the brain?

Two opposite philosophical perspectives on consciousness tried to find solutions for these problems: dualism and materialism. Dualism considers the mind and the brain as two separate phenomena, while for materialism, the mind and the brain have a pure physical nature (Dennet, 1997). Dualistic theories are based on the Cartesian idea that conscious experience does not have a physical nature and the mind and the brain are two distinct entities. According to this view, the brain has a physical structure with non-physical features. Mental phenomena, like conscious experience, emerge from brain activity, but they are not part of brain processes, indeed they are considered supra-ordinal features of the brain. Many philosophers and scientists do not support the dualistic view of the mind anymore. New evidence about a role of specific brain areas in mental phenomena (i.e. emotional state, memory and language functions) favored a materialistic view of the relation between the mind and the brain. Indeed, materialism, and more recently *functionalism,* defines mental states as the products of the interaction between functionally connected brain systems. This determines a direct link between brain activity and mental phenomena (Dennet, 1997).

Dualistic and materialist theories are object of several criticisms, because they underestimate either biological evidence or the role of subjective experience. In this context of opposite philosophical views, how to define conscious experience and how consciousness emerges from the brain are crucial issues. Indeed, recently, a new approach has been proposed to study the theme of consciousness, trying to find the solution of the dichotomy between dualism and materialism in *biological naturalism* (Searle, 2008). According to biological naturalism, consciousness is a biological phenomenon that every human being lives as a subjective experience. Thus, to understand what consciousness is, the questions about the nature of mental phenomena must be reversed, focusing on the processes underlying conscious experience. In this context, Searle (2008) proposes the *Unified Field theory*, which considers consciousness as a unified concept in a continuum between unconscious and conscious information processing. What is defined as consciousness is “access consciousness” (Searle, 2008), the fact that some of the information in our brain eventually enters our awareness and becomes a conscious and reportable content (Dehaene, Charles, King, & Marti, 2014).

The concept of “reportability” is at the center of access consciousness, which is operationalized at a cognitive level as the series of processes, which form the representation of either a stimulus or an internal state (i.e. feelings, confidence, and errors) for subjective verbalization. The strength and the quality of the subjective representation are the variables that determine whether a piece of information is or is not conscious and thus whether we can report the content of our representation (Block, 1995; Wessel, 2012). The brain’s ability to represent, manipulate and report our own mental contents is called metacognition. Metacognitive report is the main criterion to study the access consciousness (De Martino, Fleming, Garrett, & Dolan, 2013; Dehaene et al., 2014). For instance, metacognition of errors can be studied during multiple choice tasks. In these tasks, people are able to represent and evaluate their decision and responses. Indeed, they are often aware of their errors even without an explicit feedback and they can report levels of subjective confidence on their performance accuracy (for a review see Yeung & Summerfield, 2012). Intuitively, from this point of view, metacognition is virtually indistinguishable from conscious processing and this intuition has served as a basis for the frequent identification of consciousness with self-oriented metacognition (Lau & Rosenthal, 2011; Persaud, McLeod, & Cowey, 2007).

However, some processes below metacognition, such as those associated with the monitoring of one's performance (i.e. error detection) (Endrass, Reuter, &

Kathmann, 2007; Maier et al., 2011; Nieuwenhuis et al., 2001), are mostly automatized and can be implemented non-consciously. Thus, whether and how unconscious processing influences metacognitive evaluations can and should be tested empirically (Charles, Van Opstal, Marti, & Dehaene, 2013). For instance, in cognitive control, these studies can contribute to understand processes underlying error awareness and metacognition of errors.

In next paragraphs, psychophysiological research methods in neuroscience for studying consciousness and cognitive control will be reported and subsequently, the most relevant results and theories in the literature on error processing and error awareness will be reviewed.

MEASURES OF PERFORMANCE MONITORING AND CONSCIOUSNESS

Behavioral measures of error detection and error awareness

In the second half of 1960, pioneering studies on error processing (Rabbitt, 1968a; Rabbitt, 1966) described behavioral changes after errors. In these studies, participants performed speeded choice tasks (such as the Flanker task), where errors could occur. After errors, immediate response-corrections by a second key press of the correct response are often observed. This delayed correct response was interpreted as an automatic internal correction tendency after errors (Rabbitt, 1968b; Steinhauser, Maier, & Hübner, 2008). Moreover, post-error adjustments of performance are also frequently reported, as a slowing in the reaction times on subsequent correct trials (post-error slowing, PES) and as an overall post-error improvement of accuracy (PIA) (Laming, 1978). These results first evidenced mechanisms for error detection, as correction tendency and post-error adjustments.

Later, error signaling (a specific button to signal error occurrence) was also introduced to study conscious error awareness (Rabbitt, 1968b, 1990). Classically, error signaling paradigms required participants to provide a second response whenever they noticed that they committed an error. In these paradigms, participants after performing a primary task (e.g. a flanker task) are prompted to press an ‘‘error signaling button’’ whenever they think that an error occurred (Rabbitt, 1968b, 2002). An error, which is correctly signaled, is considered consciously perceived and defined as ‘‘aware error’’, whereas an error not followed by a signaling response is considered as ‘‘unaware error’’. Notably, error signaling is a measure of subjective error awareness, as it requires a secondary evaluation of the primary task response (i.e. metacognition). However, methodological limitations must be considered. For instance, under time pressure, it could happen that, although participants become aware of an error they simply do not report it (Steinhauser et al., 2008) or felt that they do not have enough time to signal it (Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010). Some of these limitations were circumvented introducing, in the secondary signaling task, the classification of all responses. In this version of error signaling, participants, after each trial of the primary task, classified all their response as correct or error (Endrass et al., 2007; Klein et al., 2007; Wessel et al., 2011). This prompts participants to systematically report their judgments on each response. Whereas error signaling is largely used to study error awareness, it is essential to consider that several factors (i.e. motivational, top-down factors and instructions) may influence error signaling criteria (Steinhauser & Yeung, 2010; Ullsperger et al., 2010). For instance, participants, assuming a low error signaling criterion, could report errors, although they are not sure.

Hence, another measure to study error awareness is confidence rating on response accuracy. These procedures have been recently introduced to investigate how sure participants are about their responses (i.e. response confidence). Different confidence rating scales have been proposed. Particularly, in the study of error awareness, Likert-scales are commonly used. For instance, Boldt and Yeung (2015) asked participant, after each response, to rate response confidence in a 6-points scale from certainly wrong to certainly correct (Boldt & Yeung, 2015). Importantly, while error signaling implies a dichotomous distinction between aware and unaware errors, ratings have the advantage to distinguish levels of subjective response confidence. Thus, confidence rating scales allow to study subjective error awareness and metacognition in a graded fashion (Windey & Cleeremans, 2015). An alternative measure to rate subjective confidence is post-decision wagering. This procedure has been already successfully used to assess visual awareness (Persaud et al., 2007). After a primary task response, participants place a bet of either a small or large amount of money on the accuracy of their responses. Post-decision wagering could improve subjective reports on confidence (Barrett, Dienes, & Seth, 2013). Indeed, while participants using numerical ratings may underestimate or overestimate their confidence, in post-decision wagering, a cash incentive can motivate accurate assessment of performance (Persaud et al., 2007). In this sense, post-decision wagering is considered a valuable measure of metacognitive abilities (Fleming & Dolan, 2010; Seth, 2008) and of subjective awareness (Persaud et al., 2007).

As error awareness can be a graded phenomenon, a new method to study different levels of error awareness was recently proposed (Di Gregorio, Steinhauser, & Maier, 2016). In the corresponding study, participants first responded to a target while ignoring different incongruent distractors (primary task) (Di Gregorio et al., 2016). Then, in a secondary error classification task, participants indicated not only whether they had committed an error, but also classified the type of distractor error they committed. In this way, errors can be distinguished based on the levels of error awareness. Indeed errors could be: unaware (i.e. errors that were not classified), partially aware, (i.e., errors that were noticed but misclassified) and fully aware (i.e., errors that were correctly classified) (Di Gregorio et al., 2016). Differently from confidence ratings, this error classification procedure does not require a direct report of subjective awareness. Indeed, this procedure allows for distinguishing levels of error awareness, based on participants' classifications.

A last consideration regards the relation between error awareness and post-error adjustments. Interestingly, some measures of post-error adjustments seem to interact with error awareness. For instance, larger post-error slowing was reported after aware errors (Nieuwenhuis et al., 2001; Rabbitt, 2002). However the results are not unequivocal, indeed other studies did not find differences between aware and unaware errors in the measures of post-error adjustments (Endrass, Franke, & Kathmann, 2005; Maier, Di Gregorio, Muricchio, & di Pellegrino, 2015).

Based on these considerations, the measure of psychophysiological brain activity during specific cognitive tasks can be useful method to study neural correlates of cognitive control and their relation with behavior. In the next paragraph, an overview on psychophysiological methods is provided with a focus on brain correlates of error processing

Cognitive psychophysiology and error processing

Since the German psychiatrist Hans Berger in 1920 discovered brainwaves, an important method to study human brain activity associated with cognitive processes has been electroencephalographic recording (EEG). The EEG is a high temporal resolution method to measure brain activity. There are several reasons to use high temporal resolution methods for studying neuro-cognitive processes (Cohen, 2014). Indeed, cognitive, perceptual, emotional and motor processes are fast and most of these processes occur within tens to hundreds of milliseconds. Moreover, processes like the emergence of conscious representation of events may occur in temporal sequences. EEG techniques allow capturing fast cognitive dynamics and thus the temporal sequences of cognitive events in the time frame in which cognition occurs. Additionally, EEG methods are non-invasive and directly measure neural activity. Indeed, the voltage fluctuations and the oscillatory brain activity measured in the EEG are direct reflections of biophysical phenomena in neuron populations (Buzsáki & Wang, 2012). Finally, EEG signals contain different types of information. For instance, EEG data can be analyzed in terms of latency, location and strength of the psychophysiological response. This multidimensional data can provide largely independent information linked to specific cognitive events.

A method for linking EEG activity to specific cognitive events is the analysis of event-related potentials (ERPs). ERPs are extracted from the continuous EEG data by calculating the synchronized means to repeated presentations of cognitive stimuli or to the execution of motor responses. When the ERPs are related to a stimulus, they are termed stimulus-locked. If instead, they are related to the execution of a response, the ERPs are termed response-locked. The most important components of the error monitoring system (i.e. Ne/ERN and Pe) are response-locked ERPs.

An alternative EEG method for studying event-related activity is the analysis of the variation of power spectrum in different frequency bands. These analyses reflect neural oscillation and can be studied as the psychophysiological response in oscillatory brain activity after cognitive events during time (time-frequency analysis). Different frequency bands can reflect different physiological mechanisms and are implicated in several cognitive functions. For example theta band (3-7 Hz) in the fronto-central sites is related with cognitive control and error processing, while alpha band (8-12 Hz) on posterior sites is related with visual processing (Cavanagh & Frank, 2014; Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009; Navarro-Cebrian, Knight, & Kayser, 2013; Romei, Gross, & Thut, 2010).

While earlier studies on error processing focused on behavioral changes after error commission, more recently, the time course and the neural substrates of error monitoring were additionally investigated. In the next sections, the most relevant theories on psychophysiological correlates of error processing that were developed within this more recent tradition will be introduced.

NEUROSCIENCE AND PSYCHOPHYSIOLOGY OF ERROR DETECTION AND ERROR AWARENESS

Fast error detection and the Ne/ERN

In recent years, error-monitoring processes were intensively studied with electrophysiological measures. Over the last three decades, a vast amount of knowledge has been gathered on functional anatomy of error processing (i.e. error detection and conscious error awareness). To study correlates of error processing, the EEG is recorded while participants perform speeded or difficult multiple responses tasks (e.g. the flanker task). In case of errors, a fronto-central negativity, the Ne/ERN is typically elicited within few milliseconds after response execution (Falkenstein et al., 1991; Gehring, Coles, Meyer, & Donchin, 1995). Functionally, the Ne/ERN has been proposed to reflect a mismatch between the intended correct response and the executed error (e.g., Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993), a post-response conflict between incompatible responses (e.g., Yeung, Botvinick, & Cohen, 2004), a prediction error signal (e.g., Holroyd & Coles, 2002) or the unexpectedness of errors (e.g. Alexander & Brown, 2011; Brown & Braver, 2005). Integrating the functional roles of Ne/ERN, it seems to reflect certain task-related features (i.e. the level of response conflict) at an early time point of error processing (Steinhauser & Yeung, 2010). Moreover, several studies also found correlations between the amplitude of the Ne/ERN and the amount of behavioral adjustments following errors (Debener et al., 2005; Maier et al., 2011; Ridderinkhof et al., 2002). Thus, Ne/ERN is often interpreted as a fast signal of error detection acting to initiate post-error behavioral adjustments (Maier et al., 2011; Ullsperger, Danielmeier, & Jocham, 2014).

Recently, error-related oscillatory brain activity was also studied as a correlate of the performance monitoring system. In particular, fronto-central theta power has been reported to be larger for errors compared to correct responses in a time window between response execution and the 200 milliseconds thereafter (Murphy, Robertson, Harty, & O'Connell, 2015; Yordanova, Falkenstein, Hohnsbein, & Kolev, 2004). Furthermore, fronto-central theta power can be modulated also in conditions of high conflict (Cohen & Cavanagh, 2011) and novelty (Cavanagh, Zambrano-Vazquez, & Allen, 2012), evidencing functional similarities with the Ne/ERN. Moreover, numerous reports proposed that the Ne/ERN is generated by a reorganization of ongoing oscillatory brain activity in the theta band in terms of transient phasic burst of activity or oscillatory synchronization (for a review, Yeung, Bogacz, Holroyd, Nieuwenhuis, & Cohen, 2007). These commonalities between fronto-central theta and Ne/ERN suggest that these signals may reflect variants of similar underlying neural processes. Indeed, modulations of fronto-central theta power (i.e. larger power for errors compared to correct responses) are often interpreted as signals of error detection (Cavanagh, Zambrano-Vazquez, et al., 2012; Murphy et al., 2015; Yordanova et al., 2004).

In the next sections the major theories on Ne/ERN (mismatch, conflict monitoring and reinforcement learning) and on error detection are exposed. Subsequently, psychophysiological correlates of conscious error awareness will be reviewed with a focus on the related functional theories.

Mismatch/Comparator theory

Early theories suggested that the Ne/ERN reflects a specific process of error detection. For this perspective, the Ne/ERN reflects a comparison process between the representation of the output of the motor system (represented by an efference copy of the erroneous action) and the best estimate representation of correct response (Falkenstein et al., 1991; Gehring et al., 1993). The representation of the correct response arises from continuous perceptual stimulus processing after response execution. According to this view, the Ne/ERN is conceptualized as a correlate of premature responses (i.e. errors), executed before stimulus processing is complete. This view was also supported by evidence of faster reaction times for errors compared to correct response in tasks like the Flanker task (Falkenstein et al., 2000). Factors influencing the representation of either the executed error or the representation of the correct response reduce the amplitude difference between the Ne/ERN and the waveform related to the correct response.

Conflict monitoring theory

A broader perspective on cognitive control suggested that the performance monitoring system monitors conflict during information processing (Botvinick et al., 1999; Carter et al., 1998). Indeed, fMRI studies evidenced that areas associated with the performance monitoring (i.e. caudal ACC regions) are activated on both error and correct trials (e.g. Carter et al., 1998; Kiehl, Liddle, & Hopfinger, 2000; Milham & Banich, 2005). More specifically on correct trials, ACC activity has been observed in conditions of high response conflict. After a response, the conflict arises when two or more incompatible response tendencies are simultaneously activated (i.e. the correct and the erroneous response tendencies; Yeung et al., 2004). Modeling analyses and ERP data showed that, the Ne/ERN reflects this post-response conflict between the representation of the correct response tendency and the executed error. Similarly to the mismatch theory, conflict monitoring theorizes that the post-error correct response tendency comes from continuous incoming information from stimulus processing. This raises corrective response tendency, which conflicts with the executed erroneous response. Thus, the Ne/ERN reflects a more general mechanism of conflict detection (i.e. the detection of post-response conflict) rather than error detection per se (Yeung et al., 2004).

Reinforcement learning theory and PRO model

Holroyd and Coles proposed the reinforcement learning (RL) theory of error processing and cognitive control (Holroyd & Coles, 2002). According to the RL theory, a prediction error is generated in the basal ganglia and in dopaminergic midbrain neurons when events worse than the expectation occur. Error commission is a specific case of an event worse than expected. Arguably, reward expectation is a central assumption of the RL theory. Expectations are developed from the history of prior reinforcements, established by the associations between stimulus-response conjunctions and action-outcome values. When the outcomes deviate from the expectation, the reward prediction error signal is conveyed in the ACC (Ullsperger, Danielmeier, et al., 2014). The Ne/ERN is the correlate of this prediction error, generated in the ACC (Holroyd & Coles, 2002). Functionally, the Ne/ERN signals events worse than expected to trigger the need for post-error adjustments (Holroyd & Coles, 2002).

An alternative theory of error processing is the “prediction of response outcome” (PRO) theory (Alexander & Brown, 2010). The PRO theory assumes that neurons in the mPFC code the learned prediction of the probability of various possible outcomes. When expected outcomes occur, the prediction error signal is inhibited, while in case of non-occurrence of expected outcomes (i.e. unexpected non-occurrence), the activity in the mPFC is maximal. Outcomes are then evaluated with respect to the deviations from the prediction and in general surprising outcomes are associated with greater activity in mPFC and with Ne/ERN. This is the major difference between RL and PRO theories. Indeed, for the RL the Ne/ERN reflects actions worse than expected, while for PRO the Ne/ERN reflects error-likelihood (Brown & Braver, 2005). For instance, the PRO theory considers the possibility that, if negative outcomes (errors) are most likely to occur, the Ne/ERN would be generated on correct trials.

Late error awareness and the Pe

As we have just reviewed, the performance monitoring system and the Ne/ERN have been intensively studied and different functional models have been proposed. However, researchers also focused on questions regarding the conscious perception of errors: How do we consciously detect that we committed an error? Which of the brain structures and psychophysiological correlates are relevant for error awareness?

Psychophysiological studies on error awareness showed that, after the Ne/ERN, at a latency of about 200–400 ms, a broader positivity over centro-parietal electrodes occurs, the error positivity (Pe) (Falkenstein et al., 2000). The Pe has been found to be correlated with error awareness (Overbeek, Nieuwenhuis, & Ridderinkhof, 2005; Steinhauser & Yeung, 2010). Indeed, in error signaling paradigms, Pe shows larger amplitude for aware errors compared to unaware errors. Moreover, the Pe is also modulated in a graded manner by the level of error awareness (Di Gregorio et al., 2016) and by confidence on error awareness (Boldt & Yeung, 2015). In a neuroanatomical and functional point of view, some authors showed a correlation between the Pe and the activity in the anterior insular and in the norepinephrine system (Ullsperger et al., 2010). In particular, the anterior insula, the norepinephrine response and the Pe appear to covary with consciously perceived errors (Ullsperger et al., 2010; Wessel et al., 2011).

Evidence accumulation and the global neuronal workspace.

While extensive researches suggest a relationship between the Pe and error awareness (for a review see Wessel, 2012), only few studies tried to address the question on the specific role of the Pe in the emergence of error awareness. For instance, Steinhauser and Yeung (2010) proposed that error awareness could be conceptualized as a decision process. Within this framework, the available evidence that an error has occurred is accumulated from different parallel processing systems (i.e. low-level evidence accumulation from sensory system, autonomous system and cognitive system) until a decision criterion is reached (i.e. high-level decision, Steinhauser & Yeung, 2010, 2012). In their study, the authors varied cash incentives to encourage participants to adopt either a low or a high criterion for signaling errors, so that a higher criterion required more evidence for error signaling. Although a higher decision criterion led to fewer aware errors, the averaged Pe for signaled and unsignalled errors were comparable in the high and low decision criteria. This result implies that the Pe does not reflect the number of signaled errors or, in other words, the output of the decision process. Notably however, a higher decision criterion was associated with larger Pe amplitudes if only signaled errors were considered. Thus, for signaled errors, the Pe varied according to the decision criteria. Specifically, larger Pe for signaled errors with a high criterion reflects larger accumulated evidence that an error has occurred (Steinhauser & Yeung, 2010). Taken together, these results suggest that the Pe is the correlate of the evidence accumulation process, which precedes the emergence of error awareness.

A crucial process within this framework is the accumulation of evidence from primary lower levels and domain specific systems. It is essential to remember that in the brain there are several domain-specific systems (i.e. sensory system, emotional system, motor system, cognitive control system) (de Lange, Jensen, & Dehaene, 2010; Steinhauser & Yeung, 2012; Ullsperger, Fischer, Nigbur, & Endrass, 2014; Wessel et al., 2011) and conscious experience emerges from their complex interaction (Dehaene & Changeux, 2011; Dehaene & Naccache, 2001). At the same time, much of the information processing in the brain occurs unconsciously or involuntarily. Thus, an important question for error awareness is to understand how the lower level unconscious information is integrated to consciously report the contents of our mental experience and behave accordingly.

A possible interpretation comes from studies on accumulation of evidence in visual awareness. In particular, the Global Neuronal Workspace (GNW) theory (Dehaene & Changeux, 2011; Dehaene & Naccache, 2001) proposes that access to consciousness depends on a flexible and long-distance global sharing of information throughout cerebral cortex (Dehaene et al., 2014). While different unconscious information is processed in parallel by specialized cortical systems, a flexible selection and sharing of relevant information allows to create coherent and conscious representation of a mental content (e.g. a stimulus or an action). Thus, conscious representations emerge from a series of stages of information processing and information sharing. In particular, evidence is accumulated until a threshold for consciousness access is reached (Dehaene & Naccache, 2001). Then, some of this information could be eventually shared within a set of interconnected high-level cortical regions (including the dorsolateral prefrontal cortex, inferior parietal cortex, mid-temporal cortex and the insula) forming a ‘global workspace’ (Dehaene et al., 2014; Ullsperger, Fischer, et al., 2014; Ullsperger et al., 2010). This system underlies cognitive mechanisms and functions like attention and working memory (Kouider, de Gardelle, Sackur, & Dupoux, 2010) and the neural connections and activity within the system are related to conscious states (Dehaene & Naccache, 2001).

The global neural workspace could be also involved in error awareness to share information about errors. Evidence for errors can be accumulated in an early stage of error processing and error awareness can emerge when this evidence exceeds the error awareness threshold (Wessel et al., 2011). The global neural workspace could integrate error evidence converging from specific lower-lever systems (including the performance monitoring system), and create conscious representations of errors (Ullsperger, Danielmeier, et al., 2014; Ullsperger, Fischer, et al., 2014; Wessel et al., 2011).

The evidence accumulation hypothesis and the role of the GNW for error awareness are largely accepted in the literature (for a review see Ullsperger, Fischer, et al., 2014). However, the specific relation between early signals of the performance monitoring system, like the Ne/ERN, and the later emergence of error awareness is under debate (Wessel, 2012). In particular, the question is open whether the Ne/ERN forms the basis and provides necessary evidence for error awareness. Two alternatives are possible: first, the information underlying the Ne/ERN is necessary for the error awareness and there is a causal correlation between Ne/ERN and aware errors (Holroyd & Coles, 2002; Yeung et al., 2004). Second, error awareness can also emerge independently from the Ne/ERN. In this last case, the Ne/ERN would rely on independent sources of information and mechanisms for error detection (Nieuwenhuis et al., 2001). Several studies investigated the relation between the Ne/ERN and error awareness, but this research has yielded mixed results.

SYSTEMS OF HUMAN ERROR MONITORING AND THE ARCHITECTURE OF THE PERFORMANCE MONITORING SYSTEM

Studies reporting a modulation of the Ne/ERN by error awareness showed larger Ne/ERN amplitudes for aware compared to unaware errors (Orr & Hester, 2012; Wessel et al., 2011) or that the neural activity in the MFC predicts whether an error is consciously perceived or not (O’Connell et al., 2007). Moreover, the modulation of the Ne/ERN amplitude has been found to resemble the modulation of the Pe for aware and unaware errors on a single trial level (Hughes & Yeung, 2011).

These similarities between Ne/ERN and Pe and the modulation of Ne/ERN amplitude in error awareness has been interpreted within a cascade-like architecture of the performance monitoring system for error detection (Dhar et al., 2011; Ullsperger, Fischer, et al., 2014; Wessel et al., 2011). According to this model, the Ne/ERN provides the basis for later conscious error awareness (Scheffers & Coles, 2000; Yeung et al., 2004) and for the Pe.

In the first study disconfirming the relation between Ne/ERN and error awareness (Nieuwenhuis et al., 2001), participants performed an anti-saccade task, followed by error signaling. Comparable Ne/ERN amplitudes were found for all erroneous saccades, irrespective of whether participants were aware or not of errors. However, the Pe amplitude was larger for aware than for unaware errors. More recently, other studies reported similar dissociations, arguing that Ne/ERN and the Pe are signals of independent systems in human error monitoring (Endrass et al., 2007; Di Gregorio et al., 2016; Maier et al., 2015). Nevertheless, the debate is still open because also a partial contribution of the Ne/ERN for the Pe and for error awareness is possible. Considering, for instance, the conflict monitoring model (Yeung et al., 2004), Ne/ERN and error detection are based on post-response conflict between the executed error and the correct response. Notably, the information contained in the Ne/ERN could be also contained in the Pe. Indeed, the general information on post-response conflict could also be a specific error detection evidence for conscious representations of errors (Hughes & Yeung, 2011). Thus, also if Ne/ERN is not directly implicated in the emergence of error awareness, Ne/ERN and the Pe can rely on similar information (Ullsperger, Fischer, et al., 2014). Although no effect on the Ne/ERN is frequently reported for aware and unaware errors, the idea of a partial contribution of the Ne/ERN in conscious error detection is still compatible with the results. In the present thesis this possibility is not excluded. However, I aim to answer to strictly related questions on the relation between Ne/ERN and Pe and between Ne/ERN and error awareness. Specifically, I investigate whether the Ne/ERN is causally related with the Pe and with the emergence of error awareness and whether Ne/ERN and Pe can also rely on different types of information for error detection.

OUTLINE OF STUDIES

Three different studies investigated behavioral measures of error detection and error-related brain activity (i.e. the Ne/ERN, the Pe and oscillatory brain activity) in different experiments and error awareness paradigms. While study 1 focused directly on the relation between Ne/ERN and Pe, study 2 and 3 investigated the subjective timing of error awareness or in other words, when the sensation to have consciously detected an error can emerge.

- Study 1. A psychophysiological approach to study the architecture of the performance monitoring system was used. The main goal was to investigate whether the Ne/ERN is necessary for the emergence of a Pe. Specifically, we studied the emergence of the Pe, in a specific condition where the Ne/ERN is prevented. The logic was: observing a Pe without previous Ne/ERN means that the Pe cannot be based on the Ne/ERN. The results showed that the Pe could be present also in the absence of the Ne/ERN, demonstrating a clear dissociation between Ne/ERN and Pe as independent correlates of human error monitoring.

- Study 2. In this study, we introduce a new theoretical framework to study the timing of error awareness. During choice tasks, people often report to have detected an error already before the erroneous action was actually executed (early error sensations). This anecdotal evidence is in contrast with the idea that conscious error detection in the brain emerges only 300 hundred milliseconds after the response (i.e. at the level of the Pe). We used different behavioral measures of error awareness to investigate how often people report early error sensations and their confidence of having experienced early error sensations. To this aim, participants were prompted to distinguish between early errors (i.e. errors accompanied by early error sensations) and late errors (i.e. errors not accompanied by early error sensations). Results show that early error sensation is a frequent and robust phenomenon during choice tasks.

-Study 3. In this last study, we combined behavioral measures and psychophysiological approaches to study the correlates of early error sensations. In particular, we studied the modulations of Ne/ERN and Pe when participants reported or not errors accompanied by early error sensations by comparing early vs. late detected errors. We hypothesized a correlation between the two components whether Ne/ERN and Pe are both similarly modulated by early error sensations. However, while the Ne/ERN was not sensitive to early error sensations, the Pe was. Thus, in the specific case of judgments on the timing of error awareness, Ne/ERN and Pe could rely on different types of information. This additionally supports the idea of independent systems in human performance monitoring.

STUDY 1: ERRORS CAN ELICIT AN ERROR POSITIVITY IN THE ABSENCE OF AN ERROR NEGATIVITY: EVIDENCE FOR INDEPENDENT SYSTEMS OF HUMAN ERROR MONITORING.

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Abstract

Errors in human behavior elicit a cascade of brain activity related to performance monitoring and error detection. Whereas the early error-related negativity (Ne/ERN) has been assumed to reflect a fast mismatch or prediction error signal in the medial frontal cortex, the later error positivity (Pe) is viewed as a correlate of conscious error processing. A still open question is whether these components represent two independent systems of error monitoring that rely on different types of information to detect an error. Here, we investigated the prediction that the Ne/ERN but not the Pe requires a representation of the correct response to emerge. To this end, we created a condition in which no information about the correct response was available while error detection was still possible. We hypothesized that a Pe, but no Ne/ERN should be obtained in this case. Participants had to classify targets but ignore flankers that were always associated with an incorrect response. Targets but not flankers were masked with varying target-masking intervals. Crucially, on some trials no target at all was presented, thus preventing the representation of a correct response and the emergence of a Ne/ERN. However, because flankers were easily visible and responses to the flankers were always incorrect, detection of these flanker errors was still possible. In line with predictions of a multiple-systems account, we observed a robust Pe in the absence of a Ne/ERN for these errors. Moreover, this Pe relied on the same neural activity as that on trials with a visible target, as revealed by multivariate pattern analysis. These findings demonstrate that the mechanisms reflected by the two components use different types of information to detect errors, providing evidence for independent systems of human error monitoring.

Keywords: error monitoring, error awareness, error positivity, error-related negativity, multivariate pattern analysis

STUDY 2: ARE ERRORS DETECTED BEFORE THEY OCCUR? EARLY ERROR SENSATIONS REVEALED BY METACOGNITIVE JUDGMENTS ON THE TIMING OF ERROR AWARENESS

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Abstract

Errors in choice tasks are not only detected fast and reliably, participants often report that they knew that an error occurred already before a response was produced. These early error sensations stand in contrast with evidence suggesting that the earliest neural correlates of error awareness emerge around 300 milliseconds after erroneous responses. The present study aimed to investigate whether anecdotal evidence for early error sensations can be corroborated in a controlled study in which participants provide metacognitive judgments on the subjective timing of error awareness. In a first experiment, participants worked on a flanker task and had to report whether errors occurred before or after the response. In a second experiment, we employed post-decision wagering to measure confidence on early error sensations. Moreover, we investigated whether reports of early error sensations are influenced by an expectation bias by setting a reference point in a preceding visual awareness task. Our data show that participants report early error sensations with a high level of confidence in the majority of error trials across paradigms and experiments, whereas no evidence for an expectation bias was found. These results provide first evidence for the existence of early error sensations, thus informing theories of error awareness.

Keywords: error awareness, error detection, metacognition

STUDY 3: PSYCHOPHYSIOLOGICAL CORRELATES OF THE TIMING OF ERROR DETECTION

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This paper is in submission

Abstract

Fast and accurate error detection is a crucial ability of human performance monitoring. Although the earliest neural correlate of error awareness, the error positivity (Pe), has been reported to emerge around 300 milliseconds after erroneous responses, it has recently been shown that, at least subjectively, error awareness can emerge considerably earlier. This phenomenon called early error sensation refers to the subjective feeling of having detected an error even before the erroneous response was executed. In the present study, we collected EEG during an error classification paradigm to track how early error sensations are reflected in neural correlates of performance monitoring. Participants first had to perform a flanker task, and then had to indicate whether an error in this task has occurred and whether this error was detected before or after response execution. EEG results showed that no error-related activity prior to the Pe was larger for early detected errors than for late detected errors, thus confirming that the Pe is the earliest neural marker of error awareness. However, early detected errors were accompanied by a reduced fronto-central theta power, an increased suppression of sensorimotor mu and beta activity, and an increased Pe. These effects could reflect that early error sensations are associated with higher error expectancy and stronger evidence for an error.

Keywords: Early error sensations, error awareness, error-related negativity, error positivity, oscillatory brain activity.

CONCLUSIONS

OVERVIEW OF STUDIES

The main goal of the present thesis was to study the psychophysiological correlates of the performance monitoring system (i.e. Ne/ERN, Pe and oscillatory brain activity) to investigate the relation between early signals (i.e. Ne/ERN) of error detection and the later signals (i.e. the Pe) of error awareness.

In study 1 we used a target masking procedure in a modified version of the flanker task (Eriksen & Eriksen, 1974). Target masking totally prevented the representation of the correct response and the Ne/ERN (Falkenstein et al., 2000; Gehring & Knight, 2000). However, achieving error awareness was still possible in case of flanker errors. Indeed, because flankers always afforded a different response than the target, a response to the flanker of the stimulus was an error. Notably, under this flanker error condition where the Ne/ERN was prevented, the Pe was still reliable. Moreover, just like the Ne/ERN, also fronto-central theta power was prevented for flanker errors in the masked target condition. Results show that the Ne/ERN does not provide necessary input to the later error awareness mechanism underlying the Pe

In study 2 we introduced a new theoretical framework to study the subjective timing of error awareness. Specifically, we studied early error sensations by comparing early and late detected errors (i.e. errors accompanied by early error sensations or not). We used different primary tasks to elicit early error sensations (e.g. flanker task and perceptual discrimination tasks). Then, we used different error awareness procedures to report and rate subjective confidence on early error sensations (error classification and post-decision wagering). Results show that participants frequently reported early errors and highly rated their confidence on having experienced early error sensations. Finally, no evidence of an expectation bias was found.

In study 3, we used a psychophysiological approach to study early error sensations. Specifically, we compared EEG correlates of the performance monitoring system for early and late detected errors. Results show that Ne/ERN amplitudes were comparable for early and late errors. However, a larger Pe emerged for early than for late errors. In the time-frequency domain, fronto-central theta power was also sensitive to early error sensations, but, differently from the Pe, theta power was reduced for early errors compared to late errors. Moreover, late sensorimotor activity was stronger following early than following late detected errors, resembling the results on the Pe. These results implicate that only Pe and sensorimotor activity, but not Ne/ERN and fronto-central theta, are related to the subjective timing of error awareness.

INDEPENDENT SYSTEMS OF ERROR PROCESSING

Our results are in contradiction with studies and accounts supporting a causal relation between Ne/ERN and error awareness and between Ne/ERN and Pe (for a review see Ullsperger, Fischer, et al., 2014). Most of studies, which reported correlations between Ne/ERN and error awareness used stimulus masking (Charles et al., 2013; Maier et al., 2008; Woodman, 2010), stimulus degradation (Scheffers & Coles, 2000), difficult perceptual discriminations (Steinhauser & Yeung, 2010) or complex and difficult tasks (Hewig et al., 2011; Shalgi, Barkan, & Deouell, 2009). These procedures make the target difficult or impossible to identify and consequentially increase the rate of unaware errors. Indeed, errors due to data limitations are frequent under such conditions. Crucially, data limitation impairs the representation of the correct response and thus directly reduces the Ne/ERN (Charles et al., 2013; Di Gregorio et al., 2016). At the same time, errors due to data limitation are also hard to detect, because without a representation of the correct response, participants have to guess whether a response was an error or not. Thus, if both reduced Ne/ERN and reduced Pe are due to a weak or absent representation of the correct response, this suggests that the relation between Ne/ERN and error awareness is correlative rather than causal.

Because data limitation is a factor influencing error processing, alternative methods were introduced to study the relation between Ne/ERN and error awareness. However, research in this field has yielded mixed results. For instance, there is evidence for a contribution of Ne/ERN to subjective error awareness (for a review see Wessel, 2012). A study by Wessel and colleagues (2011) used an anti-saccade task (see also Klein et al., 2007; Nieuwenhuis et al., 2001) and error signaling to investigate error-related brain activity and responses in the autonomic nervous system (ANS). Results showed that the Ne/ERN was larger for aware errors compared to unaware errors. Furthermore, the Ne/ERN amplitude covaried with the Pe amplitude and with changes in ongoing ANS activity (i.e. heart rate deceleration and pupil dilation). In this framework, the authors hypothesized that several systems can generate input signals (e.g. Ne/ERN, sensory input, proprioception) for the accumulation of evidence for the presence of errors. These signals contribute for the emergence of error awareness, which is reflected in the Pe (Wessel et al., 2011). In contradiction, however, recent evidence (Gibbons, Fritzsche, Bienert, Armbrecht, & Stahl, 2011; S Nieuwenhuis et al., 2001) and our previous studies reported different patterns of results for Ne/ERN and error awareness. For instance, error awareness could be preserved in patients with impaired Ne/ERN (Maier et al., 2015) and Ne/ERN and Pe could be modulated differently by the level of post-response conflict (i.e. a larger Ne/ERN was associated with a smaller Pe; Di Gregorio et al., 2016). Importantly, all these studies did not use target-masking procedures to induce errors, so that errors due to data limitation were prevented. Thus, previous studies already evidenced specific cases in which Ne/ERN and error awareness, and Ne/ERN and Pe, can covary (Wessel et al., 2011), be dissociable (S Nieuwenhuis et al., 2001) or be negatively correlated (Di Gregorio et al., 2016).

Crucially, previous works and the studies in this thesis, did not exclude the possibility that Ne/ERN could eventually covary with the Pe and with error awareness. For instance, it is possible that task-related features, like the level of post response conflict, similarly modulate both the Ne/ERN and the Pe (see also Di Gregorio et al., 2016; Hughes & Yeung, 2011). However, here we demonstrated that the Ne/ERN and fronto-central theta power do not provide necessary information for the emergence of the Pe and presumably for error awareness (study 1). Indeed, the Pe can emerge also in conditions where Ne/ERN was prevented. Moreover, in the specific case of early error sensations, the Ne/ERN was not modulated, but larger Pe was found for early errors. In particular this last result suggests that, while the Ne/ERN reflected the level of post-response conflict (see also Steinhauser & Yeung, 2010; Yeung et al., 2004), the Pe was sensitive for metacognitive judgments on the timing of error awareness (see also Boldt & Yeung, 2015; Yeung & Summerfield, 2012). This implies that early and late stages of error processing can also rely on different information during error processing. This idea is further supported by the effect on oscillatory brain activity. Indeed, opposite results patterns are shown for the fronto-central theta activity and for the later Pe. Although both brain correlates covaried with early error sensations, smaller fronto-central theta and larger Pe seem to reflect different aspects of early error sensations (i.e. error expectation and error awareness, respectively). Notably, similar dissociations can be found between fronto-central theta power and later alpha suppression on the visual system and sensorimotor activity (study 3). These results again support the idea that independent systems in human performance monitoring exist (study 1) and can rely on different types of information for error detection and compensation (study 3; Endrass et al., 2007; Navarro-Cebrian et al., 2016; Nieuwenhuis et al., 2001).

One important consideration on early error sensations is that similar early error sensations emerged on different task conditions, as on congruent and incongruent trials. Stimulus congruency can elicit different levels of post-response conflict (Yeung et al., 2004) and influence correlates of performance monitoring system accordingly (see also Hughes & Yeung, 2011; Steinhauser et al., 2008). In study 3, we considered only incongruent errors because we have too few trials in the congruent condition. Previous literature however reported already larger Ne/ERN for congruent errors (e.g. Yeung et al., 2004). Based on this evidence, it is possible to expect larger Ne/ERN also for congruent errors in study 3, but still not a modulation for early error sensations. Indeed, as study 2 shows, early error sensations are similar for congruent and incongruent trials. This could be interesting because it would show another dissociation between Ne/ERN and later awareness-related processes.

Considering that the Ne/ERN and the Pe could be functionally independent, some authors also argued that the two components have different neural generators. Anatomical studies suggest that the Ne/ERN might be generated on posterior medial frontal cortex (pMFC), in particular in caudal areas of the anterior cingulate cortex (ACC) (Bush, Luu, & Posner, 2000; Debener et al., 2005; Dehaene et al., 1994) and on dorsal ACC (Ullsperger, Danielmeier, et al., 2014). Nevertheless, literature on neural localization of the Pe is heterogeneous. While it has been demonstrated that connectivity in anterior insular cortex is enhanced after aware errors compared to unaware errors (O'Connell et al., 2007; Ullsperger, Danielmeier, et al., 2014; Ullsperger et al., 2010), there is only few evidence of a direct neural source of the Pe in the insula (Dhar et al., 2011). Instead, more studies suggested that the Pe could be generated in rostral areas of ACC (Endrass et al., 2007; Herrmann, Ro, Ehlis, Heidrich, & Fallgatter, 2004; Van Veen & Carter, 2002), an area involved in evaluative, emotional, and motivational processes. Therefore, anatomical findings seem to suggest different neural generators for Ne/ERN and Pe. While the Ne/ERN might be generated in the caudal and dorsal ACC, the Pe source localization might be localized in the rostral areas of mPFC as in rostral ACC.

To summarize, although some information could be shared by Ne/ERN and the Pe for conscious error detection (Hughes & Yeung, 2011; Scheffers & Coles, 2000), our results support the idea of independent systems for error processing. In particular, while the early stage of error processing could reflect intrinsic features of task processing (i.e. level of post-response conflict or error expectancy; Alexander &

Brown, 2011; Yeung et al., 2004), the correlates of error awareness (i.e. the Pe) emerge later within a putative evidence accumulation account for errors (Steinhauser & Yeung, 2010; Ullsperger, Fischer, et al., 2014; Wessel, 2012).

A question at this point could be: how a conscious knowledge that we committed an error is created? A possible explanation is provided in the next paragraph.

NEUROSCIENCE OF CONSCIOUS ERROR PERCEPTION: ERROR DETECTION AND ERROR AWARENESS

The most relevant interpretation for the Pe and the timing factors of conscious error detection proposes that, cerebral cortical activities in response to an error proceed for about 300 ms in order to accumulate a sufficient amount of evidence (de Lange et al., 2010; Dehaene et al., 2014) and reach a threshold for conscious error awareness (Steinhauser & Yeung, 2010; Ullsperger, Fischer, et al., 2014).

In case of errors, conscious awareness could be achieved, for instance, by matching representations of the correct and executed responses in working memory (Maier et al., 2015, 2011). The available conscious representations can be compared to detect task goal violations (Holroyd, Hajcak, & Larsen, 2006), determine whether the executed response was an error or not and take metacognitive decisions on errors (Di Gregorio et al., 2016; study 2 and 3). Importantly, study 1 showed a specific case in which stimulus masking prevented the representation of the correct response, but not error awareness. Indeed, error awareness could be achieved directly by the detection of a task goal violation (participants were instructed that a response to the flanker would be always an error) in a later stage of error processing. Goal representations in this case could be maintained active and available in working memory (see also D'Esposito, Postle, & Rypma, 2000; Di Gregorio et al., 2016; Maier et al., 2011) to achieve awareness. Specifically, the accumulated evidence can be integrated and compared in working memory (Baars & Franklin, 2003; Del Cul et al., 2009) with the representation of the task goals to consciously detect a violation (i.e. a flanker error) and take decisions about errors. Notably, similar processes are reported also in visual awareness, in which working memory plays a crucial role in conscious detection (Baars & Franklin, 2003). Patients with a deficit in the ability to actively maintain task goal information show drastic impairment in their awareness (Del Cul et al., 2009; Naccache et al., 2005; Paxton, Barch, Racine, & Braver, 2008).

In studies 2 and 3, the evidence of early error sensations poses a strong constraint on theories of error awareness. Indeed, it implies that subjective sensation to detect errors can arise already before the execution of a response and thus considerably before the Pe. Importantly, our results showed that early error sensations are frequent during choice task, thus this phenomenon can be relevant during error processing. However, our EEG study showed that only the Pe reliably reflects early error sensations (i.e. larger amplitudes for early errors). Instead, results on fronto central theta could mirror variations of error likelihood for early errors. In particular, fronto-central theta could indicate whether expectations about the occurrence of errors are violated (Brown & Braver, 2005; Nieuwenhuis et al., 2007). The smaller theta power for early errors could reflect that early error sensations occur on trials for which the expected error probability was high, or for which evidence for an error was detected already early during stimulus processing (study 3). In this sense, early error sensations can influence the evidence accumulation process. Particularly, early error sensations could increase expectancy for errors. From this perspective, early error sensations can be an anchor for more evidence accumulation and this is compatible with the result of larger Pe for early errors (study 3). However, the Pe results could alternatively suggest that early error sensations are metacognitive illusions created to synchronize metacognition (i.e. error awareness) and objective events (i.e. execution of the erroneous response, study 3; see also Libet et al., 1983, 1979). As metacognitive contents can be integrated in the evidence accumulation (Boldt & Yeung, 2015; Yeung & Summerfield, 2012), early error sensations can be an additional information that feeds into the evidence accumulation process.

Considering previous literature and present results, it is possible to hypothesize that evidence accumulation and working memory matching are relevant processes for the emergence of error awareness. Importantly, evidence accumulation can receive various inputs for error awareness as cognitive and metacognitive information (e.g. level of post-response conflict, error likelihood etc.) related to error processing (Yeung & Summerfield, 2012). Furthermore, systems contributing for error awareness can also be independent, for instance Ne/ERN, ANS, working memory based processes can also reflect different types of information and proceed in parallel. However, if one is missing (as, e.g., the Ne/ERN in our studies), evidence from other systems can still be sufficient to enable error awareness.

In the next paragraph, how correlates of error processing interact with cognitive control and behavioral adjustments will be discussed.

HUMAN PERFORMANCE MONITORING AND COGNITIVE CONTROL

Years of research evidenced a strong relation between error-related brain activity and cognitive control in terms of post-error behavioral adjustments (Di Gregorio et al., 2016; Maier et al., 2011; Steinhauser, Maier, & Steinhauser, 2017; Ullsperger, Danielmeier, et al., 2014). Error monitoring system can trigger specific post-error behavioral adaptations based on task-related demands (Egner, Delano, & Hirsch, 2007; Maier et al., 2011). For instance, the Ne/ERN has been demonstrated to correlate with measures like post-error slowing (PES) (Botvinick et al., 2001; Holroyd, Yeung, Coles, & Cohen, 2005) and post-error reduction of interference (PERI) (Ridderinkhof, 2002). Moreover, also the Pe can be correlated with post-error adjustments like PES (S Nieuwenhuis et al., 2001; Wessel et al., 2011). This suggests that the relation between Ne/ERN and post-error adjustments is rather complex and could be mediated by error awareness and Pe amplitudes (Hajcak, McDonald, & Simons, 2003; King, Korb, von Cramon, & Ullsperger, 2010; Maier et al., 2011).

For methodological reasons, here behavioral data on post-error adjustments are not reported. Indeed, in study 1 we used three different stimulus-masking intervals (240, 128 and 0 SMIs), randomly presented during the task. In order to have reliable measures of post-error behavior, like the PES, it is essential to analyze trial sequences of the same condition (e.g. trial n-1 = correct response 240 SMI, trial n = error 240 SMI, trial n+1 = correct 240 SMI) (Dutilh, Van Ravenzwaaij, et al., 2012; Dutilh, Vandekerckhove, et al., 2012). Unfortunately, in study 1 we did not have enough trials to study sequential post-error behavior in the same conditions. In study 2 and 3, the error classification procedure and post-decision wagering after the primary task could influence RT measures and accuracy on post-error trials (Ullsperger et al., 2010). Thus, we did not report post-error behavior for early error sensations.

Signatures of post-error compensations can be found on oscillatory brain activity. Indeed, suppressions of alpha power on visual cortex and of sensorimotor activity have been found to reflect post-error adjustments (Mazaheri et al., 2009; Navarro-Cebrian et al., 2013), as larger top-down control of the performance monitoring system on cortical structures (Mazaheri et al., 2009; Navarro-Cebrian et al., 2013; van Driel et al., 2012). In study 3, we analyzed alpha frequency band on visual areas and sensorimotor mu and beta. We find alpha suppression after error trials, but not a modulation for early error sensations. Similar effects for errors, but not for early error sensations were found also on the Ne/ERN. This could eventually support the idea that there is a relation between Ne/ERN and post-error EEG signatures (Navarro-Cebrian et al., 2013; Novikov et al., 2015; van Driel et al., 2012). However, sensorimotor activity (mu and beta bands), which can signal post-error adjustments on the motor system (Mazaheri et al., 2009), showed a different pattern of results. Indeed, sensorimotor activity mirrored the Pe modulation, but not the Ne/ERN, with larger suppression for early errors compared to late errors (study 3). This would imply a correlation between Pe, evidence accumulation and post-error signatures (Maier et al., 2011; Nieuwenhuis et al., 2001; Ullsperger, Danielmeier, et al., 2014).

Dissociations between Ne/ERN and Pe and the pattern of results on EEG post-error signatures speak for the hypothesis of two independent systems for post-error adjustments. Notably, a recent study proposed a two-stage account for error detection and compensations (Maier et al., 2011). This account assumes that errors are processed on an early stage preceding the Ne/ERN and on a late stage succeeding the Ne/ERN (Maier et al., 2011). The early stage is based on early task features (i.e. level of stimulus conflict) and monitors the parameters of the systems (i.e. the level of selective attention) in order to estimate the risk of specific errors. For instance, the system can detect a poor selective attentional state and thereby estimate the risk of an error due to insufficient selectivity of attention. If an error occurs, the early process triggers a large Ne/ERN, which then enables initiating specific attentive adjustments. However, the early evaluation process is based on imprecise evidence, thus, after response execution and the Ne/ERN, a late stage is started, which evaluates the error based on more reliable information. For instance, this process could detect errors from matching memory traces of the response and the stimuli (Maier et al., 2011). When needed, the late stage could eventually implement additional adjustments. Overall, our results are in line with this view. Indeed it is possible to hypothesize independent contributions of early and late stages of error processing for post-error adjustments. As the model suggests, the Ne/ERN can trigger and initiates specific adjustments after errors (Maier et al., 2011). Moreover, the later stage could operate after the Ne/ERN and eventually trigger additional adjustments when needed.

FINAL CONSIDERATIONS

Our results and evidence from the literature suggest that the architecture of the performance monitoring system is rather complex. Specifically, several studies reported a positive correlation between Ne/ERN, Pe and error awareness (Scheffers & Coles, 2000; Wessel et al., 2011), or showed that they can covary in the same direction (Hughes & Yeung, 2011). However, other studies reported negative correlations (Maier et al., 2008; Nieuwenhuis et al., 2001) and specific conditions where Ne/ERN and Pe are differently modulated (Di Gregorio et al., 2016).

Here, in study 1 we demonstrated that Ne/ERN does not provide necessary information for the Pe and error awareness. Moreover, study 2 and 3 investigated the subjective timing of error awareness, showing that Ne/ERN and Pe can be differently modulated by early error sensations. Overall, Ne/ERN seems to be modulated by intrinsic features of task processing (i.e. the level of post-response conflict, Yeung et al., 2004) while the Pe reflects error awareness as a correlate of the evidence accumulation process (Steinhauser & Yeung, 2010; Ullsperger, Fischer, et al., 2014).

The results speak for the idea that the relation between Ne/ERN and Pe is not causal and that independent systems in human error monitoring exist for fast error detection and conscious error awareness. Presumably, these systems can independently support cognitive control to initiate post-error adjustments.

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APPENDIX

Authors' contributions

Table: Contributions of the authors to the most important production steps of each study.

STUDIES	Idea/conception	Planning/conduction	Data Analyses	Writing
STUDY 1 Di Gregorio, F., Maier, M. E., & Steinhauser, M. (2018). Errors can elicit an error positivity in the absence of an error negativity: Evidence for independent systems of human error monitoring. *NeuroImage*, *172*, 427–436	FDG, MM, MS	FDG	FDG, MS	FDG, MM, MS
STUDY 2 Di Gregorio, F., Maier, M.E., & Steinhauser, M. (submitted). Are errors detected before they occur? Early error sensations revealed by metacognitive judgments on the timing of error awareness.	FDG, MM, MS	FDG	FDG	FDG, MM, MS
STUDY 3 Di Gregorio, F., Maier, M.E., & Steinhauser, M. (in submission). Psychophysiological correlates of the timing of error detection	FDG, MM, MS	FDG	FDG	FDG, MM, MS

Abbreviations: FDG = Francesco Di Gregorio, MM = Martin E. Maier, MS = Marco Steinhauser