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Error-related cardiac deceleration: Functional interplay between error-related brain activity and autonomic nervous system in performance monitoring

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ABSTRACT

Coordinated interactions between the central and autonomic nervous systems are crucial for survival due to the inherent propensity for human behavior to make errors. In our ever-changing environment, when individuals make mistakes, these errors can have life-threatening consequences. In response to errors, specific reactions occur in both brain activity and heart rate to detect and correct errors. Specifically, there are two brain-related indicators of error detection and awareness known as error-related negativity and error positivity. Conversely, error-related cardiac deceleration denotes a momentary slowing of heart rate following an error, signaling an autonomic response. However, what is the connection between the brain and the heart during error processing? In this review, we discuss the functional and neuroanatomical connections between the brain and heart markers of error processing, exploring the experimental conditions in which they covary. Given the current limitations of available data, future research will continue to investigate the neurobiological factors governing the brain-heart interaction, aiming to utilize them as combined markers for assessing cognitive control in healthy and pathological conditions.

1. State of the art

Human behavior is inherently error-prone, and the consequences of errors can be fatal in a continuously changing environment. Indeed, error detection and conscious error awareness are crucial abilities for optimizing goal-directed behavior and thus survival. As a consequence, errors trigger a cascade of autonomic nervous system (ANS), cortical, and behavioral responses, which are linked to the implementation of post-error adjustments (Agam et al., 2011; Fu et al., 2023; Ullsperger et al., 2014b). In this context, the activation of specific brain areas, concomitant changes in brain activity (Fu et al., 2023, 2019; Ullsperger et al., 2014a), in the heart rate (HR; Danev and de Winter, 1971), and in other ANS measures like pupil dilation (Maier et al., 2019; Van der Wel and Van Steenbergen, 2018) after error commission suggest an intertwined brain-body relationship during error processing.

Within brain activity measures, the error negativity or error related negativity (Ne/ERN; Falkenstein et al., 1997; Gehring et al., 2018, 1993) is one of the most extensively studied error-related components derived from Electroencephalography (EEG). The Ne/ERN is a negative deflection observed in the response-locked event-related potential (ERP), typically occurring around 50–100 ms after the execution of behavioral errors during cognitive tasks. The Ne/ERN is presumably generated in the dorsal anterior cingulate cortex (dACC; Dehaene et al., 1994), a brain area implicated in signaling the need for affective, cognitive, and autonomic regulation (Ullsperger et al., 2014a). In line with this, the neural responses in the dACC, such as the Ne/ERN, are assumed to reflect the brain's mechanisms involved in error detection and may serve as an early signal for the implementation of post-error adjustments

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(Danielmeier and Ullsperger, 2011; Maier et al., 2011). Relevant theories suggested the Ne/ERN to reflect specific error-related features such as a discrepancy between the expected correct response and the executed erroneous response (Scheffers and Coles, 2000), post-response conflict (Yeung, 2004), or a prediction error (Holroyd and Coles, 2002). Importantly, significant associations between the Ne/ERN and affective processes have also been found (Dignath et al., 2020; Koban and Pourtois, 2014). For instance, studies have shown that high negative affective traits (Hajcak et al., 2004; Luu et al., 2000) and anxiety (Hajcak et al., 2003) are associated with an increased Ne/ERN amplitude.

The Ne/ERN is followed by the error-positivity (Pe), which is a broader positivity with a parietal distribution observed 200–500 ms after errors (Falkenstein et al., 2000, 1997; Overbeek et al., 2005; Steinhauser and Yeung, 2010). Several studies have investigated whether these error-related potentials reflect the emergence of error awareness by asking participants to signal each of their errors (Rabbitt, 2002, 1968). Only the Pe has been consistently found to be larger for signaled errors compared to unsignaled errors (e.g., Endrass et al., 2012; Hughes and Yeung, 2011; Murphy et al., 2015, 2012; Nieuwenhuis et al., 2001; O'Connell et al., 2007; Shalgi et al., 2009; Steinhauser and Yeung, 2010). Thus, the Pe is widely regarded as a marker of conscious error awareness (Di Gregorio et al., 2018, 2022a; Steinhauser and Yeung, 2012; Wessel et al., 2011). Both the Ne/ERN and the Pe have emerged as robust and valuable indices for investigating cognitive control, conscious error awareness, executive functioning, and the underlying mechanisms of adaptive behavioral adjustments (Gehring et al., 2018). Consequently, the Ne/ERN-Pe complex has been extensively studied in various contexts, including response inhibition tasks, decision-making, and error monitoring within the realms of cognitive and emotional control.

While EEG correlates such as the Ne/ERN and Pe are predominant measures for investigating error processing in the central nervous system, in recent years there has been a growing interest in cardiac measures (e.g., HR and HR variability, HRV) as promising avenues to explore the peripheral nervous system. In this context, EEG provides valuable insights into brain activity and cognitive processes while cardiac measures offer a complementary perspective by examining the dynamic variations, in specific time windows, of the heartbeats frequency (i.e., HR) or the change in the time intervals between consecutive heartbeats (i.e., HRV; McCraty and Shaffer, 2015). These measures serve as proxies for the ANS regulation of cardiovascular function, reflecting the intricate interplay between sympathetic and parasympathetic influences. Cardiac functioning is influenced by cognitive and emotional processes (i.e., emotional learning) providing insights into the bidirectional communication between the brain and the cardiovascular system (Benarroch, 1993; Thayer et al., 2012; Thayer and Lane, 2009; Tortora et al., 2023). For instance, HRV has been associated with attention, emotional regulation, stress, cognitive workload (S. Battaglia et al., 2023; M. Battaglia et al., 2023; S. Battaglia et al., 2023b; Battaglia and Thayer, 2022; Forte et al., 2019; Park and Thayer, 2014; Zeng et al., 2023), and changes in HRV have been reported in several psychiatric (Chalmers et al., 2014; Clamor et al., 2016) and neurological diseases (Kim et al., 2006; Leal et al., 2021; Nicolini et al., 2020). In the context of error processing, errors elicit specific ANS and visceral responses. Specifically, cardiac decelerations following errors (i.e., error-related cardiac deceleration) have been found and interpreted as internal feedback about performance accuracy (Bury et al., 2019; Danev and de Winter, 1971; Łukowska et al., 2018; Spruit et al., 2018) and an ANS signal for emotionally negative events such as errors (Bury et al., 2019).

Therefore, by integrating EEG and cardiac measures, researchers can gain a more comprehensive understanding of the complex bidirectional communication between the central and ANS, shedding light on the intricate interdependencies between neural processes and physiological regulation (Battaglia et al., 2022; Candia-Rivera, 2022; Cortese et al., 2022; Di Gregorio and Battaglia, 2023; Ottaviani, 2018; Raimondo et al., 2017; Riganello et al., 2010; Schumann et al., 2021). In this context, Ne/ERN-Pe and cardiac measures would seem to appear as prominent research domains, offering valuable insights into the interplay between cognitive and physiological processes (Thayer and Lane, 2000). Furthermore, exploring the interrelationship between Ne/ERN-Pe and cardiac measures can provide a more nuanced understanding of cognitive processes, emotional regulation, and psychophysiological responses, leading the way for novel insights into the relationship between brain and heart during cognitive control and in pathological conditions (S. Battaglia et al., 2023; M. Battaglia et al., 2023; S. Battaglia et al., 2023a; McCraty and Shaffer, 2015).

2. Methods

In this systematic review, we discussed research articles which concomitantly considered error-related brain activity and cardiac measures during error processing to study the complex interplay between performance monitoring in the brain and the ANS (see Glossary). In particular, we aimed to investigate the variables that influence both error-related brain activity and cardiac response during error processing (e.g., result patterns across conditions). We additionally considered the correlations (e.g., correlations across participants and correlations across single-trials within participants) between the measures derived from EEG and cardiac measures (i.e., Ne/ERN, Pe, HR and HRV). We followed the Preferred Reporting Items for Systematic reviews and Meta-analyses (PRISMA) updated guidance (Liberati et al., 2009; Page et al., 2021).

We searched PubMed for research articles published in English in peer-reviewed journals until 2023. We searched terms, abstracts, and full text articles and searches were completed on 20 June 2023. The used keywords for searches were: 'Error-related Negativity' and 'Heart rate' and 'Heart rate variability'. Resulting articles were screened based on inclusion and exclusion criteria. Studies were included (inclusion criteria) if: (I) they recruited human individuals, (II) they investigated error processing during cognitive tasks and (III) reported both response-locked ERP and cardiac measures. Moreover, included experimental designs were: (I) observational, (II) case-control and (III) experimental research studies. (I) Animal studies, (II) reviews, (III) qualitative studies, (IV) case reports, (V) opinion pieces, (VI) editorials and (VII) commentaries were excluded. Additional studies were screened from the bibliography of included articles. Therefore, two independent reviewers (FDG and SB) screened titles and abstracts identified from the database searches against documented inclusion and exclusion criteria. The same reviewers then independently screened full-text articles to confirm eligibility. Any conflicting ratings were resolved through consultation. Finally, 93 abstracts were screened, and only 8 studies met eligibility criteria (Fig. 1).

3. Error-related brain activity and cardiac deceleration: story of a complex relationship

Error-related cardiac deceleration after erroneous actions was first reported in 1971 (Danev and de Winter, 1971), and this effect has been replicated in different contexts of performance monitoring (Crone et al., 2003; Fiehler et al., 2004; Somsen et al., 2000; van der Veen et al., 2004). Initially, the error-related cardiac deceleration was interpreted as a corollary of the orienting response (OR; Sokolov, 1960), which postulates a cascade of changes in ANS activity (e.g., heart rate, pupil dilation, skin conductance) in response to motivationally relevant events, such as behavioral errors. However, if error-related brain activity and cardiac measures are collected together in the same study, the intertwined relationship between error detection in the brain and ANS regulation can be examined possibly resulting in new interpretations (see Table 1).

A pivotal study conducted by Hajcak et al. (2003) examined the relationships among the Ne/ERN, the Pe, and HR. The study used a modified version of the Stroop task. During the task, healthy participants

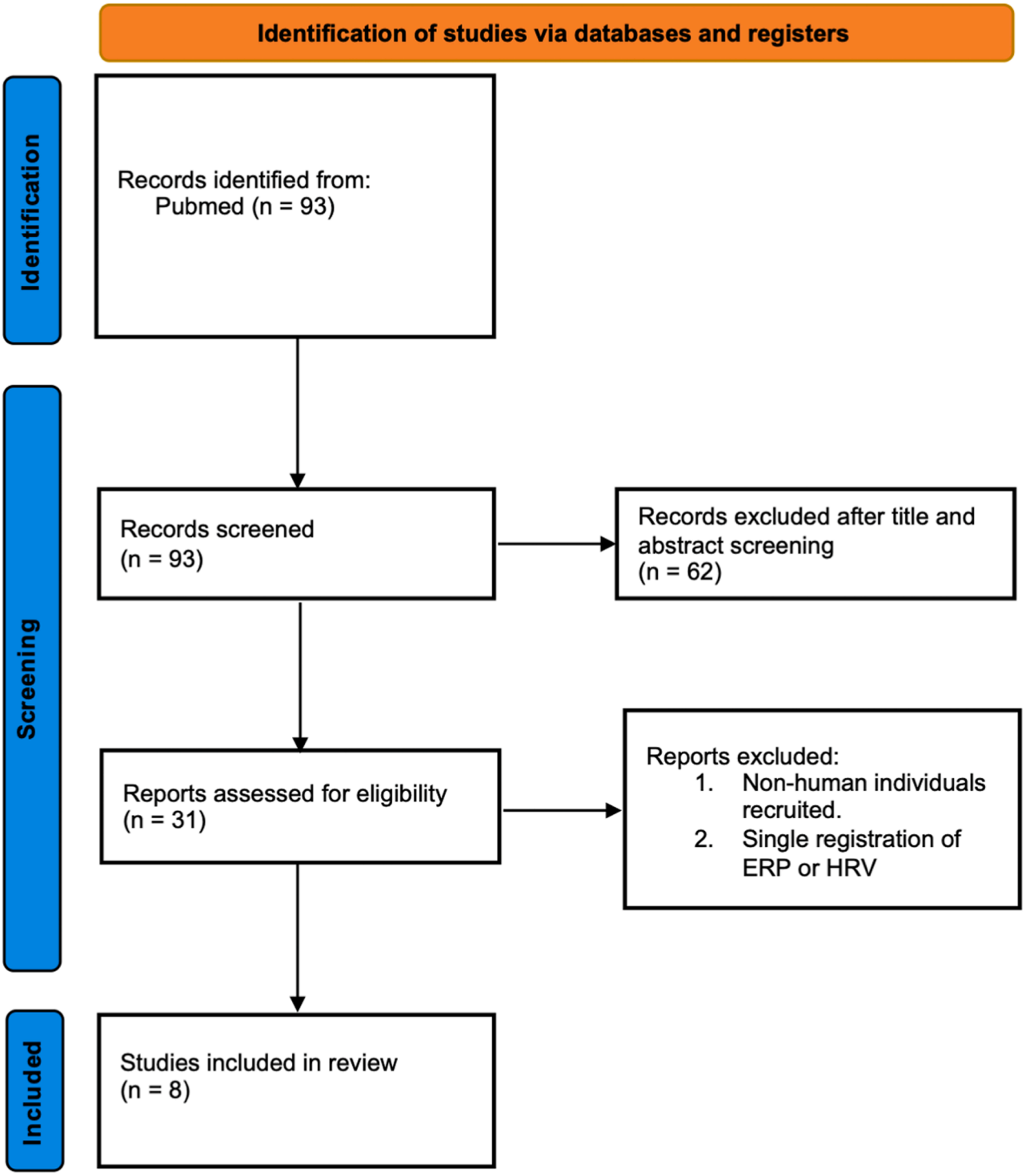

Fig. 1. Study selection PRISMA flow chart.

were presented with arrows colored either red or green, pointing to the left or right. Their instructions were to respond to the color of the stimulus by pressing a left or right key, while ignoring the direction of the arrows. This created incongruent conditions with high levels of response conflict, as the arrow sometimes indicated the opposite direction compared to the required response to the color. The results revealed that participants made more errors in the incongruent condition. Importantly, after committing an error, the typical fronto-central Ne/ERN was elicited, followed by a larger Pe for errors compared to correct trials with a central scalp distribution. Similarly, a difference between error and correct trials was reported for the HR, with stronger HR decelerations after errors, observed within a 3-second post-response time window ~~2~~. However, bivariate correlational analyses did not show any correlation across participants between Ne/ERN, Pe, and HR deceleration. Nevertheless, the authors ruled out the possibility that HR was reactive solely to conflict induced by incongruent stimuli. Thus, these results suggest that the error-related cardiac deceleration may reflect an endogenous performance monitoring response in the ANS. Specifically, the sensitivity of HR to error commission was interpreted as an interplay between emotional factors related to error commission and

Table 1
Summary of findings on Error-related brain activity and cardiac deceleration. Ne/ERN (Negativity Error/Error-related Negativity), Pe (Error Positivity), HRV (Heart Rate Variability), TSST (Trier Social Stress Test), AI (Anterior Insula), ACC (Anterior Cingulate Cortex), preSMA (pre Supplementary Motor Area).

Main Findings	Error-related cardiac deceleration. No correlation between ERN/Pe and HR	Error-related cardiac deceleration. Enhanced ERN/Pe in the high negative affect group. No differences in HRV between groups.	Error-related cardiac deceleration for aware errors. Larger Ne/ERN-Pe for aware errors	Larger Error-related cardiac deceleration in the out-group. Larger Ne/ERN for the in-group.	Ne/ERN in the anterior Insula precedes Ne/ERN over ACC and preSMA and Error-related cardiac deceleration.	Error-related cardiac deceleration and preNe/ERN preceding errors. Cardiac systolic phase predicts error-related neural activity.	Enhanced Ne/ERN in the slow-paced breathing condition. No effects on HRV.	Cardiac acceleration and smaller Pe in the stressed group.
Psychophysiological measures	Ne/ERN, Pe, HR, SCR	Ne/ERN, Pe, HR, SCR	Ne/ERN, Pe, HR, Pupil dilation	Ne/ERN, Pe, Stimulus-locked N2, HR	Intracranial Ne/ERN, HR	Ne/ERN, Pe, HRV	Ne/ERN, HRV	Ne/ERN, Pe, Stimulus-locked N2, HR
Experimental Task	Modified Stroop Task	Modified Stroop Task	Antisaccade Task with error awareness prompt	Flanker Task with in-group or out-group conditions	Stop-Signal Paradigm	Musical Sequence paradigm	Modified Flanker task during slow-paced breathing	Go/no-go task
Study	Hajcak et al. (2003)	Hajcak et al. (2004)	Wessel et al. (2011)	Pfabigan et al. (2016)	Bastin et al. (2017)	Bury et al. (2019)	Hoffmann et al. (2019)	Rodeback et al. (2020)
Participants (N)	22 (healthy participants)	60 (20 with low negative affect, 40 with high negative affect)	17 (healthy participants, Experiment 1)	20 (healthy participants) assigned to the in-group or out-group	6 (Epileptic patients)	18 (healthy professional pianist)	39 (healthy participants)	71 (healthy participants) assigned to a TSST or a relaxation training group

neurophysiological indices of performance monitoring.

In a subsequent study by the same research group (Hajcak et al., 2004), the authors further explored this affective interpretation by examining error-related activity in participants with high versus low negative affect, using the same modified version of the Stroop task. Errors were associated with both an Ne/ERN and a Pe. Additionally, the results indicated that subjects with high negative affect showed enhanced general ERP responses, both for correct and error trials, compared to subjects with low negative affect. The cardiac deceleration was specifically observed after error commission. However, no significant differences in the HR response were found between the two groups across conditions. The authors concluded that, negative affect is related to a generally increased engagement of the performance monitoring system in the brain, as evidenced by the ERP effects, while HR deceleration was only observed following error commission. Similarly, Rodeback et al. (2020), investigated how experimentally induced psychological stress influences error-related activity. In contrast to the results reported by Hajcak et al. (2004), the study found that induced negative stress only affected the amplitude of the Pe component and not the Ne/ERN. Specifically, reduced Pe amplitudes were observed in the stress group relative to the control group. This reduction in the Pe amplitude may be interpreted as decreased error awareness or reduced attention to errors in the high-stress condition. Furthermore, the results revealed an increased HR in the high-stress group, but no error-related effects were reported. In summary, these findings (Hajcak et al., 2004; Rodeback et al., 2020) suggest that although errors induced larger Ne/ERN, Pe and error-related cardiac deceleration, affective manipulations (i.e., negative affect and induced stress) revealed different effects over the Ne/ERN, Pe, and HR.

While previously presented studies (Hajcak et al., 2004, 2003; Rodeback et al., 2020) report differential effects of affective manipulations on error-related measures (i.e., Ne/ERN, Pe, HR), those studies did not specifically investigate the potentially mediating role of subjective error awareness. Indeed, how conscious error awareness is associated to the ANS response was the main focus of a study conducted by Wessel et al. in 2011. The authors employed an antisaccade task (Nieuwenhuis et al., 2001) along with simultaneous EEG, HR, and pupil dilation recordings. Participants were instructed to shift their gaze in the opposite direction of the target stimulus. Following each saccadic response, participants were asked to indicate whether they believed they had made an error or not (i.e., error awareness prompt). Consciously detected errors triggered larger Ne/ERN, Pe, and error-related cardiac deceleration compared to correct responses and undetected errors. Additionally, the HR for undetected errors showed a tendency to exhibit even less HR deceleration compared to correct trials. Similarly, pupil dilation was significantly stronger for detected than for undetected errors. This indicates that only consciously detected errors elicit the previously established error-related cardiac deceleration and pupil dilation, suggesting that conscious error perception modulates the ANS response (Ullsperger et al., 2010). The results additionally suggest that the Ne/ERN may contribute to conscious error awareness. Importantly, it was proposed that error awareness arises from a process of accumulating multimodal evidence from both the central and ANS (Wessel et al., 2011). The Pe could potentially reflect the strength of this evidence accumulation process (Di Gregorio et al., 2018, 2016; Steinhauser and Yeung, 2012, 2010). These findings, along with and the multimodal evidence account, imply a reciprocal interaction between cortical and ANS activity in conscious error processing.

A further important question is how the ever-changing dynamics of the social environment influence performance monitoring, ANS and conscious error awareness. Therefore, in a study conducted by Pfabigan et al. (2016), the authors explored how social context impacts performance monitoring correlates, ANS and behavior. Authors aimed to investigate whether a minimal group manipulation procedure, which involved assigning individuals to arbitrary group categories, would induce changes in behavioral, HR and error-related brain correlates of performance monitoring. To this aim, participants were assigned to an in-group or out-group context while performing a modified version of the Flanker task. Participants were instructed to respond to a central target and ignore distracting stimuli on the sides during EEG and HR recordings. Authors hypothesized that the group assignment would increase the salience of errors within the in-group compared with the out-group context, thus enhancing the response of the performance monitoring system. The results replicated the error-related effects on the Ne/ERN, Pe, and HR deceleration, showing larger responses for errors compared to correct trials. However, the minimal group manipulation had differential effects on these measures. Specifically, the Ne/ERN amplitudes were larger for errors within the in-group context compared

to the out-group context. On the other hand, the group context did not have an impact on the amplitudes of the Pe. Furthermore, the HR exhibited enhancement during both correct and error trials in the out-group context compared to the in-group context. This observation indicates a dissociation between the Ne/ERN, Pe, and error-related cardiac deceleration. Thus, the modulation of earlier error-related brain activity (reflected in the larger Ne/ERN) in the in-group context suggests the hypothesized sensitivity to error salience. However, the subsequent general enhancement of ANS responses in the out-group context may instead reflect intergroup bias in negative affect.

Disentangling pure saliency-driven and error-driven responses is however a complex task due to the inherent relationship between the error-monitoring and salience networks (Navarro-Cebrian et al., 2016). In many contexts, performance errors are highly salient events that can elicit emotional reactions. Crucial evidence suggests that the salience networks play a role in error detection, particularly with the involvement of the anterior insula (AI; Ullsperger et al., 2010). Indeed, the anterior insular activity is both associated with consciously perceived errors (Ullsperger et al., 2010) and the regulation of ANS responses (Chouchou et al., 2019; Ferraro et al., 2022). In line with this evidence, Bastin et al. (2017) conducted a study to examine the neurophysiological processes underlying error detection in the salience and performance monitoring networks, as well as their effects on HR. By using intracranial electrocorticography during a stop-signal task, the authors demonstrated that AI activity precedes and causally predicts responses in the ACC and in the pre-supplementary motor area (preSMA). Specifically, an Ne/ERN-like response was first elicited in the AI for error trials. Subsequently, the activity in the AI was conveyed towards the ACC and preSMA, eliciting the later peaking Ne/ERN. This may suggest that the AI detects errors as behaviorally salient events and then informs ACC and preSMA to implement compensatory mechanisms for post-error adaptations. Note, that invasive recordings in humans have shown that error-related activation of the preSMA precedes that of the ACC implying a caudo-rostral temporal gradient within the medial wall (Bonini et al., 2014; Fu et al., 2022, 2019), while the causal relationship between AI and ACC was stronger and occurred earlier than the causal relationship between AI and preSMA in the study by Bastin et al. (2017). Taken together, these results indicate that, during error processing, the AI activity precedes that of the medial wall structures, however, the exact roles of these structures in error detection and compensation and their relationships might be rather complex and more research is needed to further elucidate them. In any case, the activity in the AI-ACC-preSMA network precedes in time the error-related cardiac deceleration observed one second after error commission. In general, this data suggests that AI activity conveys information over time towards frontal and motor regions about stimulus saliency and current performance, facilitating error detection, compensation, error awareness and post-error ANS response.

At this point, a question arises: may cardiac interoceptive signals contribute to the generation of the error-related neural responses? To address this question, Bury et al. (2019) investigated whether cardiac interoceptive signals influence early neural correlates of error processing in skilled pianists performing music sequences. The study found that pitch errors were preceded by the so-called pre-error-negativity (pre-Ne/ERN), and followed by the Pe. Moreover, single trial results showed that fluctuations of the cardiac cycle influenced early error-related ERPs generated from the inferior parietal cortex. These early ERPs were larger following errors in the systolic period of the cardiac cycle compared to the cardiac diastole. This suggests that fluctuations in the cardiac cycle may influence early neural responses associated with error processing, providing evidence for a potential contribution of cardiac interoceptive signals to the generation of error-related neural activity. This finding highlights an earlier window in which cardiac afferent interoceptive information can modulate neural correlates of error processing, already before the execution of an erroneous action. This observation aligns with the results of Bastin et al. (2017) on the earlier involvement of the interoceptive monitoring in the AI during error processing. However, in contrast with previous findings, the results in this study demonstrate an error-related cardiac acceleration after error commission. Instead, the typical error-related cardiac deceleration was found to occur immediately preceding the execution of the erroneous actions, serving as a predictive information of whether the upcoming key press was an error or a correct event. This study provides significant evidence of pre-error visceral information modulating neural error-related responses. It is important to note that, in this study, errors were elicited by motor violations of memorized sequences and not by external conflicting stimuli like in the flanker task or the Stroop task. As a result, error detection signals may arise from the mismatch between the predicted action and the ongoing movements associated with errors (Di Gregorio et al., 2020, 2022a; Maidhof et al., 2009; Maidhof, 2013; Ruiz et al., 2009). These processes may occur even before action execution and can be linked to the pre-error cardiac effects on post-response error-related brain correlates.

Recently, new evidence regarding the influence of cardiac activity on error-related brain correlates has emerged from Hoffmann et al. (2019). These authors aimed to test whether a relaxation technique, specifically slow-paced breathing, can modify the neurophysiological components of error monitoring. Slow-paced breathing has previously been shown to increase cardiac vagal activity (Laborde et al., 2019; You et al., 2022) and according to the neurovisceral integration model (Park and Thayer, 2014; Thayer et al., 2012; Thayer and Lane, 2009), cardiac vagal activity influences executive functions and cognitive control. Thus, the authors hypothesized a potential effect of slow-paced breathing on the brain correlates of error detection. To test this hypothesis participants underwent respiration training before being instructed to respond to the direction of a central target arrow while ignoring distractors in a classical Flanker task. The results revealed that the Ne/ERN following errors was increased in the slow-paced breathing condition compared to a passive control condition. Furthermore, in the same slow-paced breathing condition, behavioral results indicated a decrease in response variability. However, no effects of the respiration training emerged in the Pe or in the HRV. Based on these findings, the authors argued that the brain activity is more sensitive to the experimental manipulation than cardiac vagal activity. Functionally, the amplitude of the Ne/ERN was directly influenced by the respiration rate, whereas no such effect was observed in the Pe or the HRV. Finally, these results may be attributed to the fact that respiration, through various sensory pathways, influences cortical neural activity, thereby modulating cognitive processes that ultimately impact behavioral performance (Heck et al., 2017).

4. Discussion

4.1. Brain-body interaction in error detection: functions and neuroanatomy

Committing an error activates specific ANS (i.e., error-related cardiac deceleration) and cortical responses (i.e., Ne/ERN and Pe; Bastin et al., 2017; Bury et al., 2019; Danev and de Winter, 1971; Hajcak et al., 2004, 2003; Hoffmann et al., 2019; Pfabigan et al., 2016; Rodeback et al., 2020; Wessel et al., 2011; see, Fig. 2). The investigation of the link between cortical and ANS error-related responses was the main aim of this review. Classical and recent studies on the concurrent measurement of EEG and cardiac functioning revealed promising results, suggesting that in some cases cardiac signals and error-related brain correlates may reveal brain-body interactions during error processing (Bastin et al., 2017; Bury et al., 2019; Wessel et al., 2011). In general, the results suggest that, at a cortical level, the Ne/ERN and Pe are robust correlates of error detection and error awareness within a continuous performance monitoring system (Di Gregorio et al., 2018; Gehring et al., 2018; Ullsperger et al., 2014a, 2014b; Wessel et al., 2011). At a body level, cardiac functioning and the specific error-related cardiac deceleration

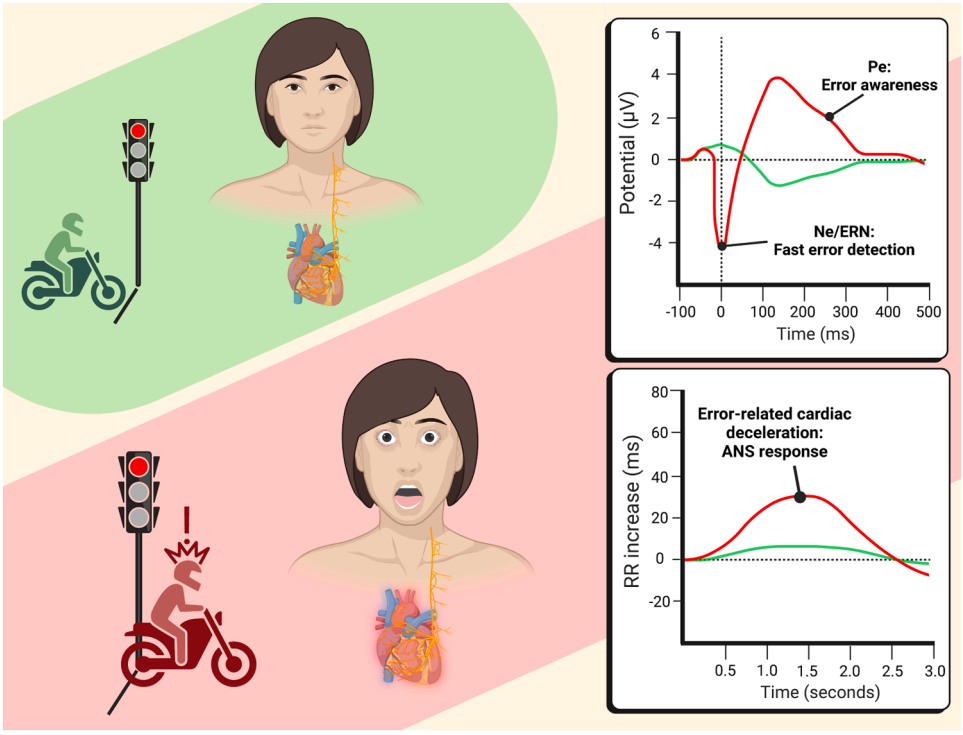

Fig. 2. Error-related brain and cardiac responses. In everyday life errors can happen and consequences of errors can be fatal. In front of a red traffic light, the correct action of the driver is to brake (upper row, left panel). However, in case of an action error (e.g., to go in front of red traffic light, lower row, left panel), at the fronto-central brain areas, the Error-related Negativity (Ne/ERN) is elicited. The Ne/ERN (red line) is a larger negative deflection compared to correct responses (green line) which reflect fast error detection. The Ne/ERN is followed by a broad later positivity (i.e., the Pe) that reflects error awareness processes (upper row, right panel). Both the Ne/ERN and the Pe have been reported to be electrophysiological markers of post-error behavioral adjustments. At the cardiac level (lower row, right panel), errors elicit a deceleration in the heart rate. This deceleration can be identified in the increase of the time interval between consecutive heartbeats (i.e., the distance in milliseconds between consecutive R peaks in the QRS complex of the cardiac activity). This phenomenon is called error-related cardiac deceleration (red line). The cardiac changes after errors reflect ANS reactions after negative events such as errors. μv = microvolt, ms = milliseconds, R = R peak in the QRS complex. The figure was created using BioRender.com.

reflect an endogenous response in the ANS after error commission (Forte et al., 2019; Łukowska et al., 2018; Takada et al., 2022). The studies presented in this review show that social and emotional factors may influence brain and body responses during performance monitoring. However, the results show differential modulation of the Ne/ERN, Pe and error-related cardiac deceleration during induced social stress conditions (Rodeback et al., 2020) and negative affect (Hajcak et al., 2004). This would implicate a possible dissociation between brain indices of error processing and ANS responses during performance monitoring. Indeed, as previously hypothesized, the modulation of earlier error-related brain activity (i.e., the Ne/ERN) could reflect specific error-related features (i.e., post-response conflict, prediction error; Yeung et al., 2004; Holroyd & Coles, 2000). Instead, the subsequent general enhancement of ANS responses after errors may reflect a reaction to negative events like errors (Pfabigan et al., 2016; Rodeback et al., 2020). Interestingly, a reciprocal interaction between Ne/ERN, Pe and cardiac phase can be found in specific tasks (Musical Sequence paradigm; Bury et al., 2019) and when considering conscious error detection. Indeed, consciously perceived errors can evoke larger Ne/ERN, Pe and error-related cardiac deceleration thus highlighting a potential mediating role of conscious error detection in the brain-heart relationship during error processing (Wessel et al., 2011). In any case, data collected to this day is still not enough to make definitive conclusions on the link between error-related brain correlates and cardiac deceleration dynamics in error processing. Based on the literature however, we can hypothesize possible functional mechanisms behind cortical-ANS association during error processing.

The found effects of affective manipulations on the Ne/ERN-Pe and error-related cardiac deceleration can be explained on the basis of some neuroanatomical considerations. It was proposed that medial prefrontal cortex may be subdivided into a more posterior portion located in dACC, which subserves primarily cognitive control functions, and an affective component, located in the rostral ACC (rACC), which is activated more in emotional contexts (Bush et al., 2000). Note that the dACC largely overlaps with the anterior midcingulate cortex (aMCC) whereas the rACC would be equivalent to pregenual anterior cingulate cortex (pACC) according to Vogt's nomenclature which is based on cytoarchitectural and receptorarchitectural studies (Palomero-Gallagher et al., 2009; Vogt et al., 1992, 2003). In accordance with the idea that ACC contributes to error monitoring, activity in this brain area is often found during error commission (Kiehl et al., 2000; Menon et al., 2001; Wittfoth et al., 2008) and source localization of the Ne/ERN revealed neural generators in both the dACC and the rACC (Buzzell et al., 2017; Luu et al., 2003). Importantly, the rACC has tight interconnections with limbic areas such as the amygdala, the orbitofrontal cortex and the AI (Devinsky et al., 1995; Ongür and Price, 2000), and mediates primarily affective (Bishop et al., 2004; Bush et al., 2000; Paus, 2001) and regulative functions (Vogt et al., 1992). The rACC and the AI are also tightly associated with ANS responses (Critchley et al., 2004; Ullsperger, Danielmeier, et al., 2014). Specifically, there are direct, indirect and causative connections between the ACC-AI network and autonomic brain stem nuclei that influence the cardiac response during performance monitoring (Critchley et al., 2003; Oppenheimer et al., 1992). Thus, an interesting possibility is that during error monitoring, the rACC and the AI constantly evaluate the state of the affective system and convey this information to the error monitoring system thereby enabling enhanced processing of emotionally relevant errors (Bury et al., 2019). Such an architecture could explain the effects of affective manipulations on the Ne/ERN-Pe

complex and on the ANS responses such as the error-related cardiac deceleration.

Although the Ne/ERN and error-related cardiac deceleration may reflect different mechanisms and responses after error commission (Hajcak et al., 2004; Hoffmann et al., 2019; Pfabigan et al., 2016; Rodeback et al., 2020), both can be related to conscious perception of errors (Wessel et al., 2011). Indeed, distributed activation of the ACC, AI and ANS was already related to conscious error awareness (Klein et al., 2007; Maier et al., 2015; Ullsperger et al., 2010). Several studies report that the activation of the AI facilitate the subjective interoception of the body responses, thus linking AI to somatic consciousness (Craig, 2009, 2002). Thus, it is plausible to hypothesize that the activity in the AI contributes both to error awareness and to cardiac responses (Ruiz Vargas et al., 2016; Ullsperger et al., 2010). Moreover, it has been assumed that AI and parts of the medial prefrontal cortex (i.e., ACC) are implicated in the response to salient events (Seeley et al., 2007). The fact that errors represent, in most contexts, salient events, could explain the functional and anatomic overlap between error-related and salience networks. But, how do salient events like errors become aware? And what are the mechanisms behind conscious error awareness? Conscious error detection can be considered the final outcome of a multimodal evidence accumulation process, where information about errors are accumulated from multiple sources of information (Dehaene et al., 2014; Dehaene and Naccache, 2001; Steinhauser and Yeung, 2012). activities in the neural networks behind both performance monitoring and cardiac responses reflect some of these multimodal evidence (Bastin et al., 2017; Steinhauser and Yeung, 2012; Ullsperger et al., 2010), which are processed during conscious error perception. The brain mechanisms of conscious error detection may integrate afferent information from the ANS and performance monitoring systems (Bastin et al., 2017; Bury et al., 2019; Dehaene et al., 2014; Dehaene and Naccache, 2001). In particular, the performance monitoring system continuously monitors different types of information and allow external (based on actions, behaviors and outcomes) and internal monitoring (based on cognitive, emotional and visceral states). In accordance, the emergence of error awareness involves the accumulation of information about task goal violations, negative outcomes, proprioception, visceral state, response conflict and emotional salient events (Alexander and Brown, 2011; Cohen et al., 2000; Di Gregorio et al., 2023, 2022b, 2018; Gehring et al., 1993; Holroyd and Coles, 2002; Steinhauser and Yeung, 2010; Trajkovic et al., 2022; Ullsperger et al., 2014a, 2014b; Wessel et al., 2011). These represent some of the crucial monitored evidence that an error has been committed. This evidence can be used to create conscious representation of errors (Dehaene et al., 2014; Dehaene and Naccache, 2001) and signal the need for increasing control (Cohen et al., 2000).

Importantly, the majority of the studies discussed in this review show a hierarchy in the time course of the brain and ANS responses during error processing (Bastin et al., 2017; Hajcak et al., 2004, 2003; Hoffmann et al., 2019; Pfabigan et al., 2016; Rodeback et al., 2020; Wessel et al., 2011). In particular, error-related effects are first shown on the Ne/ERN-Pe complex and later on the modulation of cardiac measures (i.e., HR and HRV). However, it is important to note that, Bury et al. (2019) reported that fluctuations in the cardiac cycles before error commission can anticipate the upcoming occurrence of an error and influence error-related brain activity. These results show an early time window in which afferent visceral information may influence error processing in the brain and thus error awareness. In conclusion, as also Ullsperger et al. (2014) suggested, it is still an open question whether errors trigger an ANS reaction, which then contributes to error awareness, or whether consciously perceived errors lead to ANS reactions subsequently. To answer this question direct manipulation of the level of perceptual consciousness would be needed during cognitive tasks. For instance, stimulus masking procedures are largely used in perceptual awareness to uncover how psychophysiological measures are modulated by the level of consciousness (Boldt and Yeung, 2015; Di Gregorio et al., 2022b, 2020; Trajkovic et al., 2022).

4.2. Future prospective in cognitive and clinical neuroscience

The combined use of EEG and cardiac measures holds significant potential in the study of cognitive functioning and clinical practice, offering valuable insights into the interplay between brain function and ANS regulation. EEG may provide detailed information about neural activity and cognitive processes, while cardiac measures serve as markers of ANS activity and physiological well-being (S. Battaglia et al., 2023c; Tanaka et al., 2023). Integrating these measures can enhance diagnostic approaches across various clinical domains. For instance, abnormal Ne/ERN-Pe patterns can provide indicators of underlying neurophysiological dysregulation in pathological conditions (Bailey et al., 2015; Bellato et al., 2021; Cozac et al., 2016; Holmes and Pizzagalli, 2008; Maier et al., 2015), while cardiac signals offer insights into ANS dysfunction associated with neurological diseases (Leal et al., 2021), neurodegenerative (Nicolini et al., 2020) and psychiatric conditions (Clamor et al., 2016; Koch et al., 2019; Palotai et al., 2014; Tanaka et al., 2011). Furthermore, studies investigating attention deficit hyperactivity disorder (ADHD) have already revealed alterations in the EEG activity, reduced Ne/ERN amplitudes, and atypical HRV patterns, suggesting impairments in cognitive control processes and ANS regulation (Barry et al., 2003; Bellato et al., 2021; Griffiths et al., 2017). Similarly, disruptions in the interplay between Ne/ERN and HRV have been observed in anxiety disorders, indicating potential biomarkers and targets for intervention (Chalmers et al., 2014).

In conclusion, the evidence discussed in this review aims to delve into the fascinating brain-body relationship during performance monitoring to shed new lights on the cognitive and physiological mechanisms underlying human behavior. The brain and heart markers of error processing do not always co-vary across experimental manipulations and therefore, it is currently unclear how exactly both interact. Indeed, the relationship between error processing signals in the brain (i.e., Ne/ERN-Pe) and specific cardiac measures (i.e., HR changes and HRV) is far from clear. However, the combined integration of Ne/ERN-Pe and cardiac measures holds promise in elucidating the neurophysiological mechanisms underlying cognitive control in both healthy and pathological brain. By integrating these two psychophysiological markers, researchers can gain a comprehensive understanding of how the brain's electrical activity, error processing, and ANS regulation intertwine to influence cognitive performance (Danev and de Winter, 1971; Forte et al., 2019). Finally, exploring the functional interplay between Ne/ERN-Pe and cardiac measures can provide valuable insights into cognitive disorders, mental health conditions, and potential avenues for therapeutic interventions. Therefore, by unraveling the intricate interplay between these domains, we strive to deepen our knowledge of human brain function, paving the way for advancements in neuroscience and psychophysiology human research.

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Declaration of Competing Interest

The authors declare no competing interests.

Data availability

No data was used for the research described in the article.

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GLOSSARY

Error Negativity/Error-Related Negativity (Ne/ERN): The Ne/ERN is a fronto-central negative deflection in the response-locked ERP occurring around response execution. The Ne/ERN is computed as the amplitude difference between correct and error trials and presents larger negative amplitude for error compared to correct trials.

Positivity Error (Pe): The Pe is a parietal positivity in the response-locked ERP occurring at about 200–500 ms after response execution. The Pe is computed as the amplitude difference between correct and error trials and presents larger positive amplitude for error compared to correct trials.

Heart Rate (HR): The HR is a quantitative cardiac measure computed as the frequency of heartbeats in a specific time window.

Heart Rate Variability (HRV): The HRV is a cardiac measure computed as the variation of the time interval between consecutive heartbeats.