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Joint effects of sensory feedback and interoceptive awareness on conscious error detection: Evidence from event related brain potentials

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ABSTRACT

Error awareness has been argued to depend on sensory feedback and interoceptive awareness (IA) (Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010). We recorded EEG while participants performed a speeded Go/No-Go task in which they signaled error commission. Visibility of the effector was manipulated, while IA was measured with a heartbeat perception task. The late Pe was larger for aware than unaware errors. The ERN was also found to be modulated by error awareness, but only when the hand was visible, suggesting that its sensitivity to error awareness depends on the availability of visual sensory feedback. Only when the response hand was visible, the late Pe amplitude to aware errors correlated with IA, suggesting that sensory feedback and IA synergistically contribute to the emergence of error awareness. These findings underscore the idea that several sources of information accumulate in time following action execution in order to enable errors to break through and reach awareness.

1. Introduction

Adaptive goal-directed behavior requires the ability to detect one's own errors in order to make flexible behavioral adjustments. A distinction can be made between errors that remain unnoticed and those that are consciously detected. In paradigms used to investigate error awareness, participants are usually instructed to signal the occurrence of consciously perceived errors by pressing a 'verification' button after the onset of these incorrect actions (e.g., Dhar, Wiersema, & Pourtois, 2011; Modirrousta & Fellows, 2008; Rabbitt, 1968; Rabbitt, 2002; Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010), enabling the contrast between aware and unaware errors. Impaired error awareness has been related to several clinical conditions (Klein, Ullsperger, & Danielmeier, 2013), such as attention-deficit hyperactivity disorder (ADHD; O'Connell et al., 2009; Wiersema, Van Der Meere, & Roeyers, 2009), substance abuse (Hester, Simoes-Franklin, & Garavan, 2007), schizophrenia (Mathalon et al., 2002) and autism spectrum disorder (ASD; Vlamings, Jonkman, Hoeksma, van Engeland, & Kemner, 2008), dementia (Mathalon et al., 2003), or anosognosia (Vocat, Staub, Stroppini, & Vuilleumier, 2010). Thus, the study of error awareness in healthy participants could help gain a better insight into self-regulatory problems characterizing these patient groups.

Early after error commission, a negative fronto-central deflection is observed in the event-related potential (ERP), referred to as the error-related negativity (ERN; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993) or the error negativity (Ne; Falkenstein et al., 1991), which has been source-localized to the posterior medial frontal cortex (pMFC; Debener et al., 2005; Dehaene, Posner, & Tucker, 1994). Noteworthy, the ERN is also elicited after errors that are not consciously detected and often a smaller ERN-like waveform (correct-related negativity: CRN; Ford, 1999; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000) is observed after correct responses, especially when using speeded tasks creating uncertainty regarding accuracy. Furthermore, discrepant findings regarding the modulation of the ERN by error awareness have been reported in the literature, with some studies finding no amplitude difference between aware and unaware errors (Endrass, Reuter, & Kathmann, 2007; Nieuwenhuis, Ridderinkhof, Blow, Band, & Kok, 2001; O'Connell et al., 2007), while others reported larger ERN amplitude for aware compared to unaware errors (Shalgi & Deouell, 2012; Wessel, Danielmeier, & Ullsperger, 2011; see for review Wessel, 2012).

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After error commission, the ERN is followed by a large positive wave, the error positivity (Pe). This positivity often consists of two consecutive and spatiotemporally distinct subcomponents (Arbel & Donchin, 2009; Endrass, Klawohn, Preuss, & Kathmann, 2012; O'Connell et al., 2009): an early fronto-central component ("early" Pe) followed by a later centro-parietal deflection emerging around 300–500 ms after error onset ("late" Pe). Earlier studies have unequivocally established that specifically this latter centro-parietal component is related to error awareness as it is only observed for consciously detected errors (and not for unaware errors). This is in line with earlier notions about the resemblance of the late Pe with the stimulus evoked P3b, which may reflect the emotional appraisal of an error (Dhar et al., 2011; Endrass et al., 2012, 2007; O'Connell et al., 2007; Overbeek, Nieuwenhuis, & Ridderinkhof, 2005; Wessel et al., 2011) or processing of the motivational significance of rare and distinctive or motivationally significant events, such as deviant response errors (Endrass et al., 2012; Overbeek et al., 2005; Ridderinkhof, Ramautar, & Wijnen, 2009).

According to the accumulating evidence account (Ullsperger et al., 2010), during an error trial several factors at different stages may influence whether an error will eventually be consciously detected or go unnoticed. More specifically, in the interval spanning from committing to signaling an error, an internal error signal is shaped based on several sources of information that progressively become available over time. The ERN is argued to be influenced by quickly available (motor-related) information, such as the mismatch between the efference copy and the actual response (mismatch hypothesis, Coles, Scheffers, and Holroyd, 2001) or post-response conflict (conflict hypothesis, Carter et al., 1998). In line with this notion, recently, evidence was obtained for a main generator of the ERN in the supplementary motor area, as opposed to the rostral cingulate zone (Bonini et al., 2014). According to this model, error awareness may emerge from sources of error evidence that successively become available at later stages in the post-error onset interval, namely sensory feedback (e.g., proprioceptive, auditory or visual sensory feedback), and interoceptive awareness (IA), with the latter presumably contributing to error awareness at a later stage than sensory feedback. The late Pe, as a neural correlate of error awareness, appears later during an aware error trial and these latter sources of information (i.e., sensory feedback and IA) are thus thought to mainly influence the Pe amplitude at consecutive stages following error commission, but the early ERN component to a lesser extent though. Yet, to the best of our knowledge, the influence of different sources of error evidence on the Pe as a neural correlate of error awareness has not yet been systematically investigated. The aim of the current study was therefore to explore the possible influence of two of these sources of error evidence, namely sensory feedback and IA, on the (late) Pe component (as well as the preceding ERN).

The first aim of this study was to examine the influence of visual sensory feedback from the button press on the emergence of error awareness by manipulating hand visibility of the response hand in a between-subjects design in order to avoid possible carry-over effects from one condition to the other one. Only visual sensory feedback (i.e., seeing the response finger pressing the response button) was considered and other aspects of sensory feedback, such as auditory feedback (i.e., the sound elicited by the response button) or proprioceptive (i.e., the motion or position of the response finger or effector) sensory feedback, were not manipulated and held constant across the two groups. A previously validated speeded Go/No-Go task was used in which participants were asked to signal error awareness by means of a second 'verification' button, while high-density (128 channels) EEG was recorded concurrently (Aarts & Pourtois, 2010; Dhar et al., 2011; Vocat, Pourtois, & Vuilleumier, 2008). According to the dominant model put forward by Ullsperger et al. (2010) and based on the assumption that the Pe amplitude varies according to the strength of the accumulated error evidence (Steinhauser & Yeung, 2012), participants should become less aware of their errors and show smaller Pe amplitudes under conditions of reduced sensory feedback (i.e., when the effector is not visible). We thus expected a smaller Pe amplitude to aware errors in the hand-covered condition compared to the hand-visible condition, which would also be reflected behaviorally in fewer aware errors and/or a slower error-signaling response.

The second goal of our study was to investigate the contribution of IA on error awareness. IA relates to the ability to subjectively interpret bodily signals from the autonomic nervous system (ANS) that are processed primarily in the (right) anterior insula (Craig, 2009, 2011), and is postulated to contribute directly to the emergence of the Pe (Ullsperger et al., 2010). Prior research has shown changes in autonomic activity to be specific for conscious errors. Only errors that reached awareness were accompanied by changes in autonomic activity, such as heart rate deceleration (Danev & Dewinter, 1971; Hajcak, McDonald, & Simons, 2003; Wessel et al., 2011), increase in pupil size (Critchley, Tang, Glaser, Butterworth, & Dolan, 2005), larger skin conductance responses (Hajcak et al., 2003) and increased amygdala activity (Pourtois et al., 2010). Furthermore, both IA (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004) and error awareness have been linked to enhanced activation in the (anterior) insula (Hester, Foxe, Molholm, Shpaner, & Garavan, 2005; Klein et al., 2007), which is part of the salience network (SN; Seeley et al., 2007). This network has been argued to support appropriate behavioral responses to motivationally salient events (Menon & Uddin, 2010; Pessoa, 2009) and to play a critical role in the coordination of other large scale brain networks (Uddin, 2014). Using high density EEG combined with a distributed source localization method, Dhar et al. (2011) previously found indirect evidence for insula activation to aware errors during the emergence of the Pe, as hypothesized by Ullsperger et al. (2010). These findings furthermore suggest an important role for awareness of bodily responses or signals in the emergence of error awareness. According to the model of Ullsperger et al. (2010), individuals with high IA should be more aware of their (response) errors and hence show larger Pe amplitudes for aware errors than individuals with low IA, an hypothesis that has not been validated at the empirical level yet. In the current study, we therefore sought to evaluate whether error awareness, indexed by the (late) Pe amplitude, is indeed dependent on IA. To this aim, a standard heartbeat perception task was used (Mental Tracking Method; Schandry, 1981) to assess IA. IA has been extensively measured by means of this task in the past, which rates the participants' ability to perceive their own heartbeats "consciously" (Herbert, Pollatos, & Schandry, 2007; Pollatos, Matthias, & Schandry, 2007) and substantial individual differences have been demonstrated for this ability. Critchley, Wiens, Rotshtein, Ohman, and Dolan (2004) elegantly showed that activity in the right anterior insula predicted accuracy during the heartbeat perception task and that gray matter volume in this brain region correlated with IA as well as subjective ratings of IA. Initial support for the putative link between the Pe amplitude (as measured in a Simon task) and IA (as measured by a heartbeat perception task) has recently been provided by Sueyoshi, Sugimoto, Katayama, and Fukushima (2014). These authors found a robust positive correlation between the Pe amplitude and the heartbeat perception score. However, importantly, contrary to our study, in the study of Sueyoshi and colleagues (Sueyoshi et al., 2014) awareness of errors was not explicitly measured, since aware errors were not signaled and contrasted with unaware errors. As a matter of fact, the distinction between aware and unaware errors is needed to demonstrate with high confidence the existence of a link between error awareness on the one hand and IA (as well as visual sensory feedback) on the other.

To summarize, the main aim of the current study was to investigate the influence of both visual sensory feedback and IA on the Pe and the emergence of error awareness. First, with regard to the influence of visual sensory feedback, we expected a smaller Pe amplitude to aware errors in the hand-covered condition compared to the hand-visible condition, which would also be reflected behaviorally in fewer aware errors and/or a slower error-signaling response. Second, with regard to the influence of IA, we expected participants with high IA to have more pronounced Pe amplitudes to aware errors than subjects who were less proficient in the heartbeat perception task (correlational analyses). In other words, a positive correlation was expected between scores on the heartbeat perception task and Pe amplitudes.

Importantly, we surmised these individual moderating roles of sensory feedback and IA to be significant for the late centro-parietal Pe specifically, since previous research already identified this mid latency post-error ERP component to be selectively related to error awareness, as opposed to the preceding ERN for example (Aarts & Pourtois, 2010; Endrass et al., 2012; O'Connell et al., 2007). However, we also evaluated the influence of these factors on the ERN, as some studies have reported ERN modulation by error awareness as well (Shalgi & Deouell, 2012; Wessel et al., 2011; Wessel, 2012). In addition, we explored whether and how both factors were linked to each other during the emergence of error awareness. For example, one could reason that action monitoring and error detection in the hand-covered group may depend more on interoceptive cues than the hand-visible group, due to decreased availability of exteroceptive sensory information. On the other hand, it could be that both factors build on each other towards the emergence of error awareness and that reducing visual sensory feedback (covering the hand) also hampers building up of interoceptive information. However, no directional prediction was formulated regarding the possible joint/synergistic effects of IA and sensory feedback during the emergence of error awareness since no evidence regarding their mutual influence is currently available in the literature from which specific hypotheses could be derived.

2. Methods

2.1. Participants

In both groups (hand-visible vs. hand-covered), undergraduate University students participated in exchange of 25 Euro compensation. They all signed an informed consent prior to the start of the experiment. None of the participants had a history of neurological or psychiatric problems. In the hand-visible group, the sample consisted of twenty-eight participants (age: $M = 23.07$ years, $SD = 4.13$; four males; three left-handed), while in the hand-covered group, twenty-nine students (age: $M = 22.97$ years, $SD = 5.15$; six males; three left-handed) participated. In the hand-visible group, the data of one participant were excluded due to technical problems with the recording of the EEG during the testing session. The data of another participant were excluded because of miscomprehension of task instructions. In the hand-covered group, data of one participant were excluded because of excessive blinks and alpha waves in the EEG signal. To avoid that changing task difficulties alone would confound awareness, we decided to analyze the ERP data from the difficult condition only (see description of the task). Therefore, in the hand-visible group, four additional participants were excluded due to an insufficient number of aware error trials collected for ERP analyses (<6; see Olvet & Hajcak, 2009) in the difficult condition. Results are reported for the remaining 22 participants (age: $M = 22.64$ years, $SD = 3.18$; two males, two left-handed). Likewise, due to an insufficient number of aware errors, in the hand-covered group, eight additional participants were excluded. Results are reported for the remaining 20 participants (age: $M = 21.70$ years, $SD = 2.43$; five males, one left-handed). Exclusion rate was matched between groups ($\chi^2(1) = 0.68$, $p = .41$). The experiment was approved by the local ethics committee of the Faculty of Psychological and Educational Sciences, Ghent University.

2.2. Design and stimuli

The experiments were programmed with E-Prime 2.0 software (http://www.pstnet.com/products/e-prime/) and presented on a 19-inch CRT monitor with 640×480 screen resolution (60 Hz refresh rate). Participants were seated in a sound-attenuated and dimly lit room, sitting approximately 60 cm in front of the computer screen.

2.2.1. Go/No-Go task

Stimuli were colored squares, presented on a black background and subtending 4.7 degrees of visual angle. All stimuli were presented foveally. According to the hue-saturation-value (HSV) color system, color is defined by three parameters: hue (0-360), saturation (0-100) and value (0-100). To create different tints of color, saturation and value were kept constant (both at 100), while hue was varied systematically. Two different spectra of tints were created: (a) the orange spectrum (0 to 60), with red (0) and yellow (60) as extreme colors, and (b) the purple spectrum (240 to 300) with blue (240) and pink (300) as extreme colors. A pilot study revealed that 6 participants were able to distinguish the tints of these spectra. Participants performed a Go/No-Go task, in which a cue always preceded a target. On 60% of the trials (Go trials), cue and target (Go stimulus) had the same tint, requiring a speeded button press. Possible cue-target pairs in the Go trials were red–red (0), yellow–yellow (60), blue–blue (240) or pink–pink (300). On the other 40% of trials (No-Go trials), cue and target (No-Go stimulus) differed in tint, requiring active inhibition of the prepotent response tendency.

For the No-Go stimulus, two difficulty levels (easy and difficult) were created. Easy and difficult No-Go trials were randomly intermixed. In the easy condition, cue and (No-Go) target stimuli were relatively easy to distinguish from each other. The difference in tints of cue and No-Go stimulus covered 25 points of the spectrum. Possible cue-target pairs were orange (25) – orange (50), orange (35) – orange (10), purple (265) – purple (290) and purple (275) – purple (250). In the difficult condition, the tints of the cue and (No-Go) target stimuli were harder to discriminate from one another, because the difference in tints covered only 10 points along the same spectrum. Possible cue-target pairs were red (0) – orange (10), yellow (60) – orange (50), blue (240) - purple (250) and pink (300) – purple (290). Note that No-Go stimuli were matched across conditions in that all elicited effects after the incorrect response could not be imputed to changes in the physical appearance of the stimuli across conditions.

Participants were instructed to respond as accurately and rapidly as possible when the target (Go) stimulus was physically identical to the cue (i.e., having the same perceived color) by pressing a response button on a response box with the index finger of their dominant hand, but to withhold responding when they did not match in color (No-Go). Participants were also asked to report explicitly their errors whenever they felt they had violated this simple rule (i.e., push the go button while the stimulus was actually a No-Go). Error commission had to be indicated by pressing a second 'verification' button as soon as possible following its detection (using a separate key of the response box located to the left of the main response button, to which participants had to make a lateral movement with the same response finger). Crucially, response hand visibility was manipulated between groups. In the hand-visible group, participants' response hand was

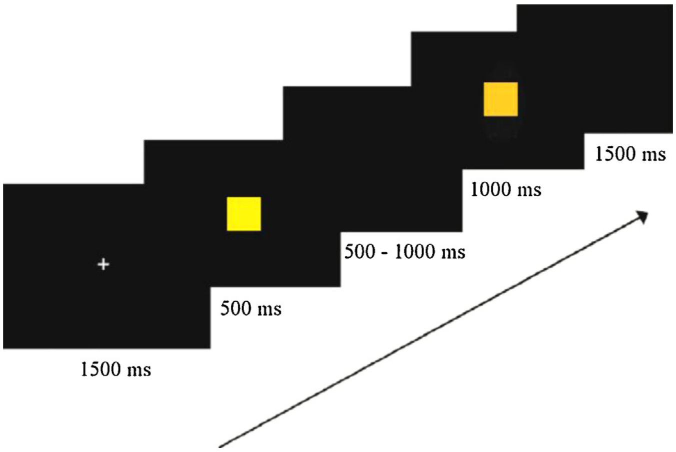

Fig. 1. Example of a No-Go trial. After error commission, participants had 1500 ms to indicate (by means of an additional key press) error awareness.

visible during the entire experimental session, while participants in the hand-covered group could not rely on visual sensory feedback from their response hand as a rectangular cardboard box covered their hand fully, starting from the wrist. For both groups, the response hand was positioned at the exact same location. Task instructions emphasized both accuracy and speed. A response limit was set for Go stimuli to induce time pressure and in turn increase error commission. At the start of every block, the initial response limit was set at 350 ms. For every participant individually, the limit was adjusted by means of an algorithm and updated online for every trial. This algorithm has already been used previously extensively (Aarts & Pourtois, 2010; Dhar et al., 2011; Koban, Pourtois, Vocat, & Vuilleumier, 2010; Pourtois et al., 2010). In short, the current RT is compared against the updated RT limit, which corresponds to the average of this RT and the preceding RT. If the participant happens to respond above this limit ("slow" hit), a negative feedback is presented, while if he happens to respond below this limit ("fast" hit), no feedback is presented (see below).

Due to the manipulated difficulty of the No-Go trials and the induced time pressure, the task resulted in a sufficient number of aware errors and unaware errors, in addition to hits. Aware errors were defined as responses to No-Go stimuli that were followed by overt reporting (i.e., verification button was pressed). Unaware errors were defined as responses to No-Go stimuli that were not followed by overt detection (i.e., no key press of the verification button was registered). Hits were defined as correct responses to Go stimuli, regardless of their actual speed (fast and slow hits were collapsed; see Aarts, De Houwer, & Pourtois (2013) for a similar approach). Omissions were defined as omitted responses to Go stimuli.

A trial started with a white fixation cross (visual angleof 0.5 degrees) presented for 1500 ms, after which the cue appeared for 500 ms. Before target presentation, a delay was introduced with a random duration between 500 and 1000 ms, precluding its anticipation. The target remained visible until a response was given, with a maximum duration of 1000 ms. After target presentation, the course of the trial depended on the identity of the target (Go or No-Go). When the participant made a fast hit or omitted a response to a Go stimulus, a black screen was shown for 1500 ms. In case of a slow hit, after a delay of 500 ms, a feedback screen indicating that participants were too slow was presented for 500 ms. When participants withheld responding to a No-Go stimulus, the black screen was presented again. In case of an error, they had 1500 ms to press the verification button during which a black screen was presented (see Fig. 1).

Twelve practice trials were administered at the beginning of the experiment to familiarize the participants with the manipulation of tints and to ensure they understood the instructions properly. In the hand-covered group, participants performed the twelve practice trials without covering of the response hand. The task consisted of 6 blocks, each block containing 36 Go trials and 24 No-Go trials, with a total number of 360 trials (216 Go trials, 72 No-Go trials in the easy condition, 72 No-Go trials in the difficult condition). A short break was introduced between two consecutive blocks. The total duration of the experimental session was about 35 min.

2.2.2. Heartbeat Perception Task

In both groups, we used the Mental Tracking Method proposed by Schandry (1981), which is widely used to assess IA, is well validated and reliable (Cronbach's alpha: .69-.90) and has a good test-retest reliability (Jones, Collins, Dabkowski, & Jones, 1988). It was administered twice, at the beginning and the end of the testing session. During this task, participants were encouraged to focus on their own cardiac activity and instructed to silently count the number of heartbeats within three separate intervals randomly varying in length. The intervals lasted for 25, 35, and 45 s and the start and end of the interval were indicated by a soft start and stop tone. It was stressed that they were not allowed to take their pulse or use any other bodily cues to facilitate counting. After the stop signal, participants verbally reported the number of counted heartbeats during a resting period of 30 s. Participants were not informed about the length of the intervals and were not given feedback on their performance. A heartbeat perception score was calculated, following standard practice (Herbert et al., 2007; Pollatos, Herbert, Matthias, & Schandry, 2007), according to this formula: 1/3 Σ (1–(|recorded heartbeats – counted heartbeats|)/recorded heartbeats). Per interval, a difference score of the number of recorded and counted heartbeats was created, which was in turn divided by the number of recorded heartbeats, subtracted from 1, summed and averaged by the number of intervals. This way, the heartbeat perception score could vary between 0 and 1, with high scores indicating small differences between recorded and counted heartbeats and in turn a high IA.

The electrocardiogram (ECG) was recorded analogous to the EEG through external electrodes attached to the upper and lower left rib cage. R-waves were detected offline via a custom-made R-top algorithm.

2.3. EEG acquisition and data reduction

The electroencephalogram (EEG) was continuously recorded at a sampling rate of 1024 Hz with a 128-channel Biosemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands). The signal was referenced online to a CMS-DRL ground. Vertical EEG was recorded from infraorbital and supraorbital electrodes placed in line with the pupil of the right eye, while horizontal EEG was acquired through electrodes positioned on the outer cantus of each eye. Data was recalculated offline against the average reference and down-sampled to 512 Hz sampling rate. A low pass filter of 80 Hz (48 dB/oct), a high pass filter of 0.05 Hz (48 dB/oct) and a 50 Hz Notch filter were applied. By means of the method of Gratton and colleagues (Gratton, Coles, & Donchin, 1983) the signal was corrected for blinks. ERPs of interest were computed offline with Brain Vision Analyzer 2.0 (Brain Products, GmbH, Munich, Germany). Segmentation was performed relative to response onset with an interval ranging from 200 ms before to 1000 ms after response onset. Each segment was baseline corrected to the entire pre-response onset interval. Artifacts were semi-automatically detected and rejected with a ± 100 μV criterion relative to baseline. Noisy electrodes were interpolated using a spherical spline procedure (order of spline = 4). The amount of noisy electrodes interpolated never exceeded 10% of the total number of electrodes (Keil et al., 2014), with a range of 0–12. We computed individual averaged data for correct (hits) and incorrect responses, separately for aware and unaware errors. Finally, a 30 Hz low-pass filter (48 dB/oct) was applied to the individual averaged data. Grand average waveforms were computed separately for the three conditions (hits, aware errors, unaware errors).

2.4. Data analysis

2.4.1. Performance

For commission errors, a mixed ANOVA with outcome (2 levels: aware errors and unaware errors) as within-subjects factor and group (2 levels: hand-visible vs. hand-covered) was performed. For the RT data, a mixed ANOVA with outcome (3 levels: hit RT, aware error RT and unaware error RT) as within-subjects factor and group (2 levels: hand-visible vs. hand-covered) was performed. Furthermore, independent samples t-tests were used to compare the hand-visible group with the hand-covered group for the other performance measures. As we had clear a priori predictions regarding the verification RT (hand-covered > hand-visible), a one-tailed t-test was used.

2.4.2. Electrophysiological measures

In accord with previous studies investigating error awareness (Dhar, Wiersema, & Pourtois, 2011; O'Connell et al., 2009), an early negative deflection (ERN) was clearly generated at FCz for all three conditions, while, as expected, a late Pe was elicited specifically for aware errors at more posterior leads along the midline, including CPz. Thus, based on the obvious topographical properties of the current data set as well as earlier ERP studies using similar task settings (see Dhar et al., 2011), the mean amplitudes of the ERN and late Pe were calculated, respectively, between 0 and 100 ms at FCz, and 300–500 ms at CPz following error commission.

First, to compare our ERP results with findings from previous studies investigating error awareness and to test the influence of hand visibility on error awareness, we performed a mixed ANOVA with the within-subjects factor outcome (3 levels: hits, aware errors and unaware errors) and the between-subjects factor group (2 levels: hand-visible and hand-covered) separately for the ERN amplitude at FCz and the late Pe amplitude at CPz. When sphericity assumptions were violated as indicated by a Mauchly test, Greenhouse-Geisser corrections were used. Amplitude values of the ERN and Pe for aware errors vs. unaware errors, aware errors vs. hits, and unaware errors vs. hits were submitted to a priori planned and orthogonal contrasts with Bonferroni corrections. If a group by outcome interaction was apparent, a paired samples t-test was applied per group comparing activity to aware versus unaware errors, in line with our specific research question, concerning the modulation of the Pe (and ERN) by error awareness. In addition, independent samples t-tests on the difference scores between outcomes (aware errors minus unaware errors, aware errors minus hits, unaware errors minus hits) were performed.

Visual inspection of the ERP data suggested a modulation of the ERN by error awareness at more posterior sites (Cz and CPz), dependent upon the availability of sensory feedback (see Fig. 2), In the hand-visible condition, a conspicuous ERN to aware errors but not to unaware errors was observed at Cz and CPz. In contrast, in the hand-covered condition, no such modulation of the ERN by error awareness was seen. Instead, error awareness seemed to emerge later in time, as an enhancement of the Pe amplitude was observed in the hand-covered compared to the hand-visible group. Based on these important observations, an additional mixed ANOVA was performed with outcome (3 levels: hits, aware errors and unaware errors) and electrode (Cz, CPz) as within-subjects factors and group (2 levels: hand-visible and hand-covered) as a between-subjects factor for ERN. When sphericity assumptions were violated as indicated by a Mauchly test, Greenhouse-Geisser corrections were used. Bonferroni corrected t-tests were applied. Again, if a group by outcome interaction was apparent, a paired samples t-test was applied per group comparing activity to aware versus unaware errors. Fig. 2 shows the grand average waveforms at FCz, Cz and CPz, for hits, aware errors, and unaware errors, separately for the hand-visible and hand-covered group.

Table 1
Behavioral data for the hand-visible and hand-covered group.

Performance data	Hand-visible group	Hand-covered group
Hit RT	288 (24)	289 (19)
Number of aware errors	13.7 (4.6)	14.4 (7.1)
Number of unaware errors	39.9 (13.4)	43.2 (13.2)
Omissions	9.8 (17.1)	2.5 (2.6)
Aware error RT	282 (35)	278 (20)
Unaware error RT	304 (43)	307 (32)
Verification median RT	571 (121)	643 (147)

2.4.3. Correlations

Correlational analyses were performed between IA on the one hand and the behavioral or neurophysiological correlates of error awareness on the other hand to shed light on the role of IA in the emergence of error awareness. As we had clear a priori predictions about the direction of these correlations (see Introduction section), one-tailed p-values were reported.

3. Results

3.1. Behavioral data

Behavioral data are reported in Table 1, separately for the two groups. For commission errors, a significant main effect of outcome was revealed ($F(1, 40) = 100.61$, $p < .001$, $\varepsilon = 0.99$, $\eta_p^2 = .72$). Both groups had significantly more unaware errors than aware errors ($p < .001$). The interaction between outcome and group was not significant ($F(1, 40) = 0.23$, $p = .64$, $\eta_p^2 = .01$).

Outcome also showed a main effect for RT ($F(2, 80) = 20.67$, $p < .001$, $\varepsilon = 0.88$, $\eta_p^2 = .34$). For both groups, a longer RT for unaware errors than for hits ($p < .001$) or aware errors was evidenced ($p < .001$). A marginally significant RT difference between hits and aware errors was observed ($p = .08$). The interaction between outcome and group did not reach significance ($F(2, 80) = 0.46$, $p = .63$, $\eta_p^2 = .01$).

Furthermore, a marginally significant group difference was found for omissions ($t(40) = 1.91$, $p = .06$, $d = 0.60$), bearing in mind that very few omissions were made (see Table 1). Importantly, in line with one of our predictions, the between-group comparison of the median verification RT yielded a significant difference ($t(40) = -1.72$, $p = .05$, one-tailed, $d = -0.53$), with a delay in the error signaling response in the hand-covered group compared to the hand-visible group.

3.2. Electrophysiological measures

With regard to the ERN at FCz, the main effect of outcome ($F(2, 80) = 0.44$, $p = .52$, $\varepsilon = 0.53$, $\eta_p^2 = .01$), the main effect of group ($F(1, 40) = 0.55$, $p = .47$, $\eta_p^2 = .01$), and the interaction between outcome and group did not reach significance ($F(2, 80) = 0.03$, $p = .97$, $\eta_p^2 < .01$).

For the late Pe at CPz, a significant main effect of outcome was found ($F(2, 80) = 19.16$, $p < .001$, $\varepsilon = 0.61$, $\eta_p^2 = .32$). The amplitude of the late Pe was significantly larger for aware errors than for hits ($p = .001$) or unaware errors ($p < .001$). The main effect of group did not reach significance ($F(1, 40) = 0.00$, $p = .99$, $\eta_p^2 < .001$), but a

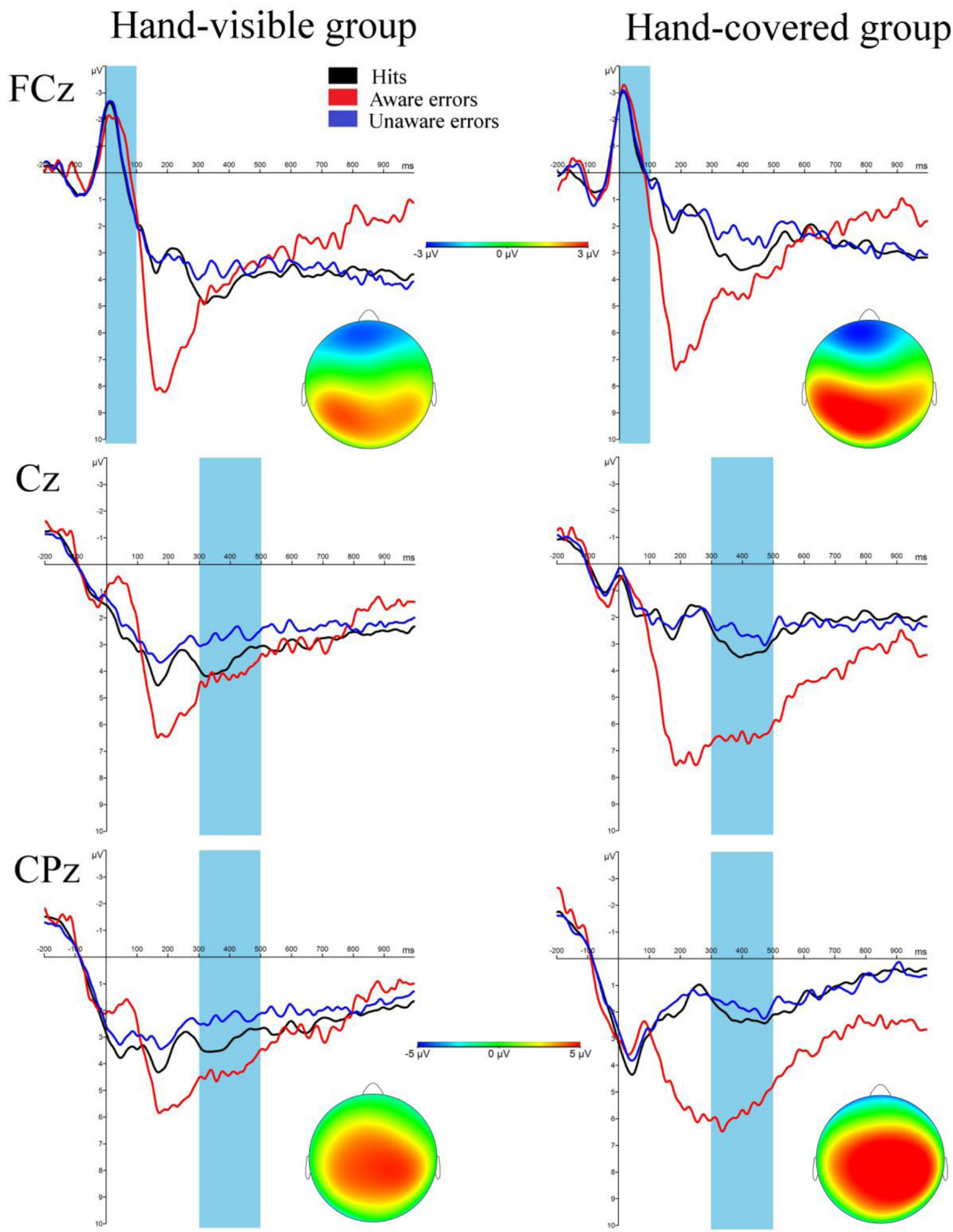

Fig. 2. Grand average waveform at FCz, Cz and CPz for hits, aware errors and unaware errors, separately for the hand-visible and hand-covered group. The topographical maps (horizontal view) correspond to the time windows of the ERN for aware errors (0–100 ms) and the Pe for aware errors (300–500 ms).

significant interaction between group and outcome ($F(2, 80) = 3.36$, $p < .04$, $\eta_p^2 = .08$) was found. Follow-up paired t-tests showed a significant difference for Pe amplitudes for aware versus unaware errors in the hand-covered group ($p < .001$, $d = 1.05$) as well as in the hand-visible group ($p = .016$, $d = 0.56$). Further, in the hand-visible condition, no difference was found between the late Pe to hits and aware errors ($p = .22$, $d = -0.28$), while the late Pe for hits was larger than for unaware errors ($p = .02$, $d = 0.58$). In the hand-covered condition, the amplitude of the late Pe to aware errors was larger than for hits ($p = .001$, $d = -0.96$), while no difference was found for the late Pe between hits and unaware errors ($p = .16$, $d = 0.33$). In addition, an independent samples t-test performed on the difference scores between aware and unaware errors indicated a marginally significant group difference ($t(40) = -1.69$, $p = 0.09$, $d = -0.52$). Moreover, the aware errors-hits difference was marginally significant between the two groups ($t(40) = -2.02$, $p = 0.05$, $d = -0.62$), while the unaware errors-hits difference was not ($t(40) = -1.11$, $p = 0.27$, $d = -0.34$).

The seemingly stronger error awareness effect at the Pe level in the hand-covered compared to the hand-visible group condition may be explained when considering the pattern of results found for the ERN at the electrodes Cz and CPz. Visual inspection of the ERP data (see Fig. 2) suggests a modulation of the ERN at more posterior sites by error awareness, dependent upon the availability of sensory feedback. In the hand-visible group, a clear ERN to aware errors but not to unaware errors was apparent, compared to the hand-covered group, in which a small negativity of equal size was elicited to aware errors, unaware errors and hits. In the hand-visible group a smaller Pe amplitude was evidenced, while a more pronounced Pe to aware errors was noticed in the hand-covered group, which suggests that error awareness seemed to emerge later in time in the latter condition (see Fig. 2).

We therefore performed an additional mixed ANOVA with outcome and electrode (Cz, CPz) as within subject factors and group as between-subjects factor, to better understand this dependency on availability of sensory feedback of the ERN modulation by error awareness (at these specific centro-parietal electrode sites along the midline). A main effect of outcome was found ($F(2, 80) = 6.86$, $p = .01$, $\varepsilon = 0.59$, $\eta_p^2 = .15$). The amplitude of the ERN for aware and unaware errors was significantly larger than the corresponding CRN elicited for hits (respectively $p = .01$, $p = .01$), while no significant difference was found between aware and unaware errors ($p = .22$). The interaction between group and outcome, however, showed a trend-significant effect ($F(2, 80) = 2.38$, $p = .10$, $\eta_p^2 = .06$). As none of the interactions with electrode were found to be significant, values of Cz and CPz were collapsed in the follow-up analyses. These analyses revealed that in the hand-visible group, the ERN to aware errors was significantly larger than to unaware errors ($p = .04$, $d = -0.46$), while this was not the case in the hand-covered group ($p = .76$, $d = -0.07$). Further, in the hand-visible condition, the amplitude of the ERN to aware errors was larger than for hits ($p = .01$, $d = 0.68$). The ERN amplitude to unaware errors was larger than the corresponding CRN elicited for hits ($p = .01$, $d = 0.66$). In the hand-covered condition, no significant difference was found between the CRN to hits and the ERN to aware errors ($p = 0.25$, $d = 0.26$), while a marginally significant difference was found between the CRN to hits and the ERN to unaware errors ($p = .07$, $d = 0.45$). Hence, the findings suggest that the ERN was modulated by error awareness, but only in the hand-visible condition.

3.3. Interoception and error awareness

3.3.1. Performance on heartbeat perception task

For both groups, the heartbeat perception score acquired at the beginning of the session (hand-visible: $M = .57$; $SD = .17$, hand-covered: $M = .69$; $SD = .20$) correlated significantly with the

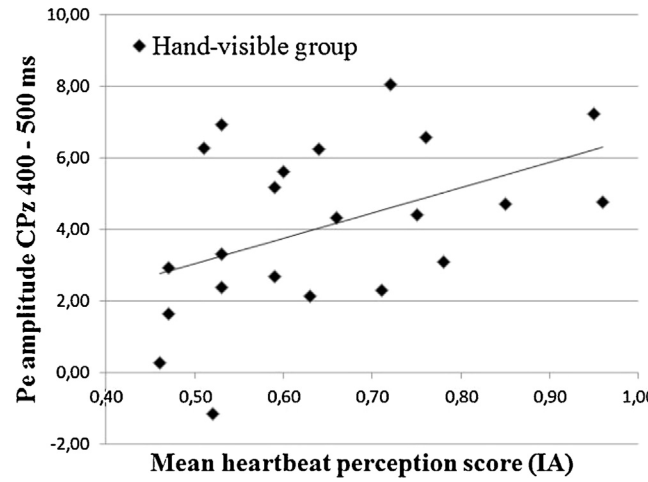

Fig. 3. Scatter plot depicting the correlation across subjects between mean heartbeat perception score (IA) and mean Pe amplitude to aware errors at CPz (bin 400–500 ms), for the hand-visible group only.

heartbeat perception score obtained at the end (hand-visible: $M = .72$; $SD = .16$; $r = .69$, $p < .001$; hand-covered: $M = .71$; $SD = .21$; $r = .86$, $p < .001$), indicating that the estimate of IA was reliable. Moreover, mean heartbeat perception scores obtained in this study were comparable to previous studies (Herbert et al., 2007; Pollatos et al., 2007). For the hand-visible group, the mean heartbeat perception score was .65 ($SD = .15$; range: .46–.96), while it was .70 (SD = .20; range: .34–.94) in the hand-covered group. The between-group comparison in mean heartbeat perception score yielded no significant results ($t(40) = -1.05$, $p = .29$, $d = -0.28$).

3.3.2. Correlations: interoception and awareness RT

Correlational analyses between the number of aware errors and median verification RT, and the mean heartbeat perception score were performed. The correlation between the mean heartbeat perception score and the number of aware errors did not reach significance, in none of the two groups (hand-visible group: $r = -.29$, $p = .099$, hand-covered group: $r = .16$, $p = .26$). Visual inspection by means of a scatter plot showed that an outlier distorted the marginally significant correlation between the mean heartbeat perception score and the number of aware errors in the hand-visible group. After removal of this outlier, the correlation was no longer trend significant ($r = -.13$, $p = .28$). In the hand-covered group, a significant negative correlation was observed between the median verification RT and the mean heartbeat perception score ($r = -.42$, $p = .03$), while no such correlation was evident in the hand-visible group ($r = -.02$, $p = .46$). However, a Fisher z test revealed that the difference between both correlation coefficients was not significant ($p = .21$, two-sided).

3.3.3. Correlations: interoception and the late Pe

To explore at what moment in time following response onset IA could be related to the emergence of error awareness, the mean amplitude of the late Pe to aware errors was broken down into two consecutive bins of 100 ms (bin 1: 300–400 ms, bin 2: 400–500 ms after error commission) and these time bins were correlated with the mean heartbeat perception score. In the hand-visible group, at time bin 2 (400–500 ms), the Pe amplitude at CPz was significantly positively correlated with the mean heartbeat perception score ($r = .45$, $p = .037$; Fig. 3), but this was not observed in the hand-covered group ($r = -.21$, $p = .19$). A Fisher z test showed that these correlations differed significantly ($p = .04$, two-sided). Moreover, this association was found to be specific for the late Pe, as the correlation between IA and the ERN to aware errors at FCz, Cz and CPz was not significant (hand-visible: all r's < |.18|, all p's > .42; hand-covered: all r's < |.35|, all p's > .13). These findings demonstrate that, as expected, participants who had higher IA showed larger Pe amplitudes to aware errors than participants with lower IA, with the strongest effect appearing between 400 and 500 ms after error commission. However, surprisingly, this effect was only observed when sensory feedback from the response hand was available, suggesting a possible interaction effect between sensory feedback and IA during the emergence of error awareness.

4. Discussion

The goal of the current study was to assess whether visual sensory feedback from the response hand and IA might each contribute to foster error awareness. To this end, high-density EEG was recorded while participants performed a speeded Go/Nogo task in which they signaled error commission by means of an extra button press, following standard practice. Hand visibility of the response hand was manipulated between subjects. IA was assessed by means of a standard heartbeat perception task (Herbert et al., 2007; Pollatos et al., 2007). At FCz, the CRN (hits) and ERN (response errors) were equally large, an observation that was compatible with previous studies using speeded paradigms similar to the one used in this study (Dhar et al., 2011; Vocat et al., 2008). The speeded nature of the task and in particular the use of a stringent response deadline (Aarts & Pourtois, 2010; Aarts, Vanderhasselt, Otte, Baeken, & Pourtois, 2013; Dhar & Pourtois, 2011) probably caused participants to be relatively impulsive and hence uncertain about their action at the time of their onset, a factor which has been shown to enhance the CRN amplitude (Pailing & Segalowitz, 2004). In line with many earlier findings in the psychophysiology literature (Dhar et al., 2011; Endrass et al., 2007; O'Connell et al., 2007; Shalgi, Barkan, & Deouell, 2009), we found that the Pe was clearly related to error awareness, being larger for aware errors than for unaware errors. Contrary to our predictions, we found a trend-significantly larger awareness effect (aware minus unaware errors) for the late Pe amplitude when sensory feedback from the response hand was not available. However, this finding seemed to be related to the observation that when visual sensory feedback was available, error awareness may have modulated the preceding ERN component, while only the Pe was modulated by error awareness when the hand was not seen, suggesting that error awareness likely emerged later in time in this condition, as reflected by an enhanced Pe amplitude (and delayed error signaling RT). These Pe results should however be carefully interpreted, as the effect for the Pe was only trend-significant. In addition, caution is needed regarding the interpretation of the ERN results (because error awareness was found to influence the early response-locked ERP signal at central, as opposed to more fronto-central sites, like FCz or Fz where this component usually reaches its maximum amplitude, as observed here as well). Nevertheless, the findings suggest that the sensitivity of the ERN component to error awareness (at least at Cz and CPz) may actually depend upon the availability of sensory feedback from the response hand, as the ERN modulation by error awareness was only seen when the hand was visible (see also here below in the discussion). Furthermore, supporting our second hypothesis, the Pe amplitude to aware errors was found to be related to the extent of IA. Participants with higher IA showed larger Pe amplitudes to aware errors than participants who were less accurate at the heartbeat perception task. Crucially, this was only observed when visual sensory feedback from the response hand was available to the participants, which dovetails with the assumption that both sources of information interact dynamically during the emergence of error awareness.

4.1. The effect of sensory feedback on error awareness

In line with the accumulating evidence account (Ullsperger et al., 2010), the Pe amplitude seemed to be influenced by the availability of visual sensory feedback from the response hand. However, contrary to our predictions, the awareness effect tended to be larger when the response hand was not visible. This may be explained by a systematic modulation of the preceding ERN component by error awareness, dependent on the availability of sensory feedback. When the information from the response hand was available, the ERN (at Cz) was modulated by error awareness. In case of reduced availability of visual sensory feedback, the ERN was not sensitive to error awareness and may have caused error awareness to emerge later in time, which in turn increased the Pe amplitude to aware errors. This result therefore confirms that error awareness may stem from a complex accumulation of evidence process, whereby the lack of an important source of information (regarding error awareness) influences the speed with which this process eventually emerges following action execution. This finding also implies therefore that participants likely needed more time to become aware of their errors, when an otherwise important source of information regarding error commission was omitted, as indirectly confirmed by the verification RT results. Although it remains unclear how this accumulation of evidence precisely operates following error onset to yield the conscious detection of these behaviorally relevant events, our ERP study is among the first to hint at a possible mechanism underlying this utmost important mental process. Here we showed that becoming aware of errors may actually be dependent upon visual sensory feedback from the response hand, in interaction with IA processes, suggesting that these two sources of information did contribute to brain mechanisms responsible for the conscious detection of response errors.

The finding that the ERN was found to be larger for aware errors, but only when visual sensory feedback from the response hand was available, indicates that ERN modulation by error awareness may depend upon this factor. ERN elicitation was influenced by a source of error evidence (namely visual sensory feedback) available only later in time, thus contradicting Ullsperger's model (2010) that posited that the ERN component is only influenced by quickly available sources of error evidence (e.g., mismatch between the efference copy and the actual response, Coles et al., 2001; or post-response conflict, Carter et al., 1998). The ERN modulation by error awareness in the hand-visible condition was however noticed at more posterior sites (Cz and CPz) than where the ERN typically reaches its maximum amplitude (FCz or Fz). This finding may suggest that early action monitoring at the level of the ERN (with a main pMFC source) would be immune to error awareness (even though this interpretation is currently debated in the literature), while error awareness would be accompanied by the activation of another, partly overlapping component, expressed more posteriorly (Cz), which could be compatible with the involvement of additional posterior cingulate regions, besides the pMFC (Agama et al., 2011; Charles, Van Opstal, Marti, & Dehaene, 2013; Wittfoth, Küstermann, Fahle, & Herrmann, 2008).

The observation that ERN amplitude modulations by error awareness partly depend on the availability of visual sensory feedback is valuable because it may help reconciling in part inconsistent findings reported in the literature regarding the sensitivity (or the lack thereof) of this early response-locked ERP component to error awareness (Dhar et al., 2011; Maier, Steinhauser, & Hubner, 2008; Nieuwenhuis, Aston-Jones, & Cohen, 2005; Wessel, 2012). Our results suggest that these inconsistencies may not only stem from methodological differences in assessing (at the subjective level) error awareness (Shalgi & Deouell, 2012), but they could also very well be imputed to systematic variations across these earlier ERP studies concerning the availability or amount of visual sensory feedback at the time of action execution. Indirect support of an influence of sensory feedback on the ERN amplitude may come from a few studies comparing processing of self-generated errors with errors that were not self-generated (observed errors). van Schie, Mars, Coles, and Bekkering (2004) compared self-generated errors with observation of errors made by others and found an ERN for both types of errors, but the ERN was reduced and delayed for observed errors. In a study by Gentsch, Ullsperger, and Ullsperger (2009), it was found that only self-generated errors evoked an ERN, while errors caused by technical malfunction elicited an FRN, which is a negative deflection consistently observed after feedback when outcomes are worse than expected (Holroyd & Coles, 2002).

4.2. The effect of interoception on error awareness

In line with our predictions, we also observed a significant negative correlation between verification RT and heartbeat detection scores, suggesting faster errors detection for those with better IA. It has to be noted though that this correlation was only significant when the response hand was not visible. However, a Fisher z test showed that these two correlations were not statistically different from each other (hand-visible condition vs. hand-covered condition), casting doubt on the condition-specificity of this relationship. Future studies including larger samples might help to resolve this issue.

More straightforward was the relationship between the late Pe (for aware errors, selectively) and IA in the hand-visible condition. A positive correlation was found between the Pe amplitude and the mean heartbeat perception score at the centro-parietal electrode CPz at approximately 400 ms following error commission. This result is in line with the recent findings from Sueyoshi et al. (2014) who reported a positive correlation between the Pe amplitude and the heartbeat perception score. However, in our study, we took error awareness into account (while these authors did not in their study), enabling us to unequivocally establish a link between the Pe amplitude, error awareness, and IA. This association was found to be specific for the late Pe, as the ERN to aware errors was not found to correlate with IA in our study. Sueyoshi et al. (2014) previously found an association between the ERN amplitude and the heartbeat perception score, but only when faces expressing disgust were presented and not when neutral faces or objects were presented. According to these authors, disgust faces probably evoked a physiological reaction, causing ERN amplitude and IA to be associated, which led them to assume a flexible and situation-specific link between error monitoring and physiological monitoring. By comparison, no emotional stimuli were presented in our task. The fact that the late Pe correlated with IA in our study fits the assumption of Ullsperger's model (Ullsperger et al., 2010) that sources of error evidence that become available at late stages after error commission, namely IA, may have an influence on "late" correlates of error detection, namely the late Pe, as opposed to the earlier ERN for example. More generally, our new findings accord with the notion that only the later centro-parietal P300-like component (which shares many similarities with the late Pe) is affected by arousal, is sensitive to salience, reflects awareness and may capture affective or motivational effects related to it (Endrass et al., 2007; O'Connell et al., 2007). In agreement with this interpretation, several theories previously advocated (e.g., Koban & Pourtois, 2014; 'somatic marker hypothesis', Bechara, Damasio, & Damasio, 2000; accumulating evidence account, Ullsperger et al., 2010) that IA plays a key role in the (conscious) processing of motivationally significant events, which is supported by research on emotion processing (Herbert, Herbert, & Pollatos, 2011; Herbert et al., 2007; Pollatos et al., 2007), and more recently, in relation to decision-making. For example, only for participants who were proficient in the heartbeat perception task was neural activity in the right anterior insula associated with better performance in the Iowa Gamblink task (Werner et al., 2013). Our study adds to this growing literature by showing a unique link between IA and a well-validated electrophysiological correlate of error awareness (Pe), suggesting that the extent to which human participants become aware of their response errors depends, at least in part, on how well they are usually able to consciously perceive autonomic bodily signals.

4.3. Interaction between sensory feedback and interoception

The fact that no (positive) correlation was observed between the late Pe (for aware errors) and IA in the hand-covered condition suggests that IA supports the emergence of error awareness only when sensory feedback from the response hand is available. In other words, error awareness (late Pe effect) depends on interoceptive information that presumably builds on or adds to the information provided by visual sensory feedback concurrently. Nonetheless, both factors do not seem to work fully independently from each other towards the emergence of error awareness. Our findings rather hint at a weakening of the contribution of interoceptive information to this process when visual sensory feedback is removed. As such, our new findings inform about the complex interaction effect at stake between exteroceptive sensory feedback and IA during the conscious detection of response errors. Earlier studies focusing on bodily awareness already provided indirect support for an interaction effect between exteroceptive and interoceptive signals (Ainley, Tajadura-Jiménez, Fotopoulou, & Tsakiris, 2012; Suzuki, Garfinkel, Critchley, & Seth, 2013), which are integrated "online" by the anterior insula (Craig, 2007; Dhar et al., 2011; Simmons et al., 2013). Nonetheless, more research is needed to explore the possible boundaries of this synergistic effect during error awareness.

4.4. Clinical implications

The finding that both sensory feedback and IA support the emergence of error awareness not only stresses the importance of better considering their modulatory roles during action monitoring from a methodological or theoretical point of view, but it may also help better understand abnormal action monitoring processes arising in specific psychopathologies that are characterized by deficiencies in error awareness, including ADHD (O'Connell et al., 2009; Wiersema et al., 2009) drug addiction (Hester et al., 2007), schizophrenia (Mathalon et al., 2002), anxiety (Aarts & Pourtois, 2010), depression (Aarts, De Houwer, & Pourtois, 2013; Aarts, Vanderhasselt, & Otte et al., 2013), ASD (Vlamings et al., 2008), dementia (Mathalon et al., 2003), anosognosia (Vocat et al., 2010), and traumatic brain injury (TBI; Hester et al., 2012). In some cases, these impairments might stem from noisy interoceptive or sensory feedback information that in turn blur or delay the conscious detection of response errors. By disentangling the specific contributions of these two important sources of information during error awareness, our findings may contribute to a better understanding of impaired action monitoring and error awareness accompanying these different disorders, which may eventually help optimize treatment options for them.

4.5. Limitations

Several limitations have to be mentioned. First, the use of an extra error-signaling response to titrate error awareness has been criticized previously, because it likely entails additional cognitive and attentional processes besides error awareness (for a thorough discussion of this issue, see Ullsperger et al., 2010). However, this standard procedure has been used extensively in many studies previously in the literature and it provides consistent ERP findings (i.e., selective modulation of the Pe component as a function or error awareness). Second, contrary to our predictions, the reduced availability of sensory feedback from the response hand had no influence on the number of aware errors signaled by the participants. This lack of group difference could be imputed to the use of a stringent response limit/deadline adjusted to the performance of the participant, that probably reduced inter-individual variability and caused all participants to make a relatively balanced amount of unwanted response errors. Third, the between-subjects manipulation of response hand visibility does not allow to fully disentangle the specific contribution of each separate factor (sensory feedback and IA) to the emergence of error awareness. To overcome this problem, future studies should implement a fully orthogonal design and perform regression analyses to uncover the relative contribution of each factor. Fourth, it cannot be excluded that manipulating hand visibility may have caused participants to press the response hand with reduced (or alternatively enhanced) force in the hand-covered condition or to pay less attention to the hand and that this has led to decreased processing of proprioceptive information instead of hand visibility itself. Accordingly, future research is needed to clarify whether visual sensory feedback (in combination with IA) influences error awareness directly, or instead indirectly via some changes in proprioceptive inputs. The observation that a typical ERN can be elicited following errors in a completely deafferented patient (Allain, Hasbroucq, Burle, Grapperon, & Vidal, 2004) suggests however that proprioceptive information does not contribute directly to early error detection. Fifth, this study was confined to clarify effects of visual sensory feedback and interoception on error awareness and other potentially important factors, such as auditory sensory feedback, were therefore not considered in the present case. Further research is warranted to examine the influence of other unexplored sources of error evidence, such as auditory sensory feedback, on the emergence of error awareness.

4.6. Conclusion

The present study sought to test the prediction that sensory feedback and IA each supports the emergence of error awareness. Replicating earlier studies (Dhar et al., 2011; Endrass et al., 2007; O'Connell et al., 2007; Shalgi et al., 2009), we found that the late Pe was related to error awareness. Contrary to our predictions, the awareness effect of the Pe amplitude tended to be larger when visual sensory feedback from the response hand was not available (versus when it was). This effect may be explained by an earlier modulation of the response-locked ERP signal by error awareness (at the level of the ERN), which depends on the availability of visual sensory feedback. Our findings lend support to the second hypothesis by showing that participants who were more interoceptive aware (as measured using an independent and standard heartbeat perception task) had in turn larger Pe amplitudes to errors inadvertently committed during a (separate) speeded Go/No-Go task that were eventually overtly detected. Crucially, this correlation was only observed when sensory feedback from the response hand was available, which confirms that sensory feedback and IA interact dynamically during the emergence of error awareness, as previously put forward in the literature (Ullsperger et al., 2010). As such, this study adds to the growing literature showing that action monitoring and (conscious) error detection do not simply involve motor or premotor control processes in the human brain, but also include a component related to the conscious processing of bodily signals. Finally, these new findings may also fuel research on neurological or psychiatric disorders characterized by impaired error awareness, including ADHD or addiction.

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