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Neural correlates of error processing reflect individual differences in interoceptive sensitivity

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ABSTRACT

Although self-monitoring is an important process for adaptive behaviors in multiple domains, the exact relationship among different internal monitoring systems is unclear. Here, we aimed to determine whether and how physiological monitoring (interoception) and behavioral monitoring (error processing) are related to each other. To this end we examined within-subject correlations among measures representing each function. Score on the heartbeat counting task (HCT) was used as a measure of interoceptive awareness. The amplitude of two event-related potentials (error-related negativity [ERN] and error-positivity [Pe]) elicited in error trials of a choice-reaction task (Simon task) were used as measures of error processing. The Simon task presented three types of stimuli (objects, faces showing disgust, and happy faces) to further examine how emotional context might affect inter-domain associations. Results showed that HCT score was robustly correlated with Pe amplitude (the later portion of error-related neural activity), irrespective of stimulus condition. In contrast, HCT score was correlated with ERN amplitude (the early component) only when participants were presented with disgust-faces as stimuli, which may have automatically elicited a physiological response. Behavioral data showed that HCT score was associated with the degree to which reaction times slowed after committing errors in the object condition. Cardiac activity measures indicated that vigilance level would not explain these correlations. These results suggest a relationship between physiological and behavioral monitoring. Furthermore, the degree to which behavioral monitoring relies on physiological monitoring appears to be flexible and depend on the situation.

1. Introduction

Self-monitoring is essential for adapting behavior in dynamically changing environments. When determining its functional significance, it is important to note that it is implemented on multiple levels, ranging from social (evaluating how other people see oneself) and mental (reflecting the contents of one's own mind) to behavioral (monitoring one's actions) and physiological (sensing visceral activity) domains. Functional neuroimaging studies have shown that different types of self-monitoring share roughly overlapping neurocognitive substrates, particularly medial cortical structures and some frontal regions, suggesting their commonality (Damasio, 1999; Luu and Tucker, 2004; Northoff and Bermpohl, 2004). However, the exact relationship among the different types of internal monitoring remains largely unclear. Here, we examined whether and how physiological and behavioral self-monitoring (both occurring at basic sensorimotor levels) are associated with each other.

Physiological monitoring of the state or sensations of the internal body is referred to as interoception, and can be considered to be the most basic level of self-monitoring. Because most information from visceral organs does not usually surface to consciousness, interoception with subjective experience can be called interoceptive awareness. In human psychological studies, interoceptive awareness has frequently been investigated in terms of cardiac perception (Cameron, 2001; Wiens, 2005), which is popularly assessed using the heartbeat counting task (HCT; also referred to as the heartbeat tracking task). In this task, individuals explicitly count their own heartbeats during a given period, and their accuracy is used as a measure of cardiac awareness (Herbert et al., 2007; Schandry, 1981). Performance on the HCT is also a useful measure of individual differences in general interoceptive sensitivity. For example, studies have demonstrated that HCT score is positively correlated with affect-related traits such as the subjective intensity of emotional experience (Herbert et al., 2007; Pollatos et al., 2007b; Wiens et al., 2000) and sensitivity to affective information (Katkin et al., 2001; Werner et al., 2009; Wölk et al., 2013). This measure has also been used to show that several clinical conditions such as panic, anxiety, depression, as well as some psychosomatic disorders, are associated with altered interoceptive processes (Cameron, 2001; McNally, 1990; Paulus and Stein, 2010). Additionally, neuroimaging and

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neurological studies have revealed that interoception is subserved by a network including the anterior cingulate cortex (ACC) and anterior insula cortex (AIC), as well as somatosensory cortex and subcortical regions (Critchley et al., 2004; Khalsa et al., 2009; Pollatos et al., 2007a). Particularly, AIC is considered to play a key role in the subjective feeling or awareness of one's internal states (Craig, 2003; Critchley et al., 2004; Terasawa et al., 2013).

Self-monitoring also occurs at the behavioral level (referred to as behavioral monitoring, performance monitoring, or action monitoring) and is crucial for adequately regulating behaviors. Detecting errors in one's own actions, or conflicts that lead to those errors, is an essential component of behavioral monitoring, which is thought to comprise a number of sub-processes such as gathering information from efferent and sensorimotor cues, detecting or deciding errors of commission, and updating or adjusting behavioral control (Nieuwenhuis et al., 2001; Steinhauser and Yeung, 2010). These processes can take place either consciously or subconsciously (Ullsperger et al., 2010).

Analysis of event-related potentials (ERPs) is a frequent technique used in the study of error processing. Two well-investigated ERPs, error-related negativity (ERN) and error positivity (Pe), are observed as deflections in scalp potential immediately after an erroneous response. ERN is an early negative component located over the frontocentral region that peaks around 50–100 ms and Pe is a later positive deflection located in centroparietal regions with a latency of about 300–500 ms (Falkenstein et al., 1990; Gehring et al., 1993). Although several hypotheses regarding the processes reflected by the two components have been proposed, they are generally accepted to manifest in different stages of error processing cascades (early and late). ERN may reflect response conflict or the early detection of internal cues signaling that an error has been made (Falkenstein et al., 1990; Gehring et al., 1993; Hughes and Yeung, 2011), while Pe may reflect a later stage that is influenced by motivational or conscious factors (Leuthold and Sommer, 1999; Overbeek et al., 2005; Ridderinkhof et al., 2009). In particular, Pe is known to be modulated by awareness of error commission (called “error awareness”; Overbeek et al., 2005; Endrass et al., 2005, 2007; O'Connell et al., 2007; Shalgi et al., 2009; Murphy et al., 2012). Unlike Pe, whether ERN reflects error awareness remains unclear owing to conflicting reports of its covariation with error awareness (Nieuwenhuis et al., 2001; Scheffers and Coles, 2000; Wessel, 2012). Individual differences in these components have been widely examined and used in clinical fields. For example, reduced ERN amplitude has been observed in individuals with ADHD, impulsivity, and low socialization (Dikman and Allen, 2000; Liotti et al., 2005; Pailing et al., 2002), while the components tend to increase in individuals with obsessive–compulsive disorder, anxiety, or negative affect (Fitzgerald et al., 2005; Hajcak et al., 2003; Santesso et al., 2006).

Electrophysiological and neuroimaging studies have reported that error processing is associated with activity in posterior medial frontal regions (particularly dorsal ACC) and AIC, as well as prefrontal and parietal cortex (Hester et al., 2005, 2004; Klein et al., 2007; Ullsperger and von Cramon, 2003). A number of studies have suggested the dorsal ACC is robustly active in error trials, and is probably a source of the ERN (Debener et al., 2005; Dehaene et al., 1994; Mathalon et al., 2003; Van Veen and Carter, 2002). The AIC has recently been reported to correlate with subjective awareness of error commission (Klein et al., 2013, 2007), and is a candidate modulator, or at least a concomitant, of Pe amplitude (Klein et al., 2007; Ullsperger et al., 2010).

Although physiological self-monitoring and behavioral self-monitoring have largely been investigated independently, the advances described above mention three points suggesting an important linkage between these two processes. First, they both reflect individual differences in affect-related traits. For example, individuals with high anxiety or negative affect tend to have both higher levels of interoceptive sensitivity and greater magnitudes of error-related ERPs than those with normal anxiety levels and affect. Second, the two processes share neural substrates, particularly the ACC and AIC. Because of the large overlap in neural substrates, physiological self-monitoring and behavioral self-monitoring are likely to be associated. Third, recent investigations have suggested that the AIC contributes not only to interoceptive awareness, but possibly also to the modulation of Pe amplitude and error awareness. Additionally, committing errors is known to be associated with physiological changes such as lowered heart rate (HR), increased electrodermal activity (Crone et al., 2003; Hajcak et al., 2003), and altered pupil diameter (Critchley et al., 2005; Wessel et al., 2011). These lines of evidence suggest that interoception (physiological monitoring) is coupled with error processing (behavioral monitoring). This association should benefit individuals. For example, by perceiving interoceptive states (e.g. being tired, sleepy, or too excited) in addition to the discrepancy between a goal and an actual motor execution, we can better correct and adjust our actions, making behavioral control more effective. Although this much is known, whether and how inter-domain coupling occurs still remains to be determined.

Some studies have suggested that within the executive control system that includes behavioral monitoring, social-emotional processes and cognitive (i.e. non-emotional) processes recruit partially different neural substrates (Bush et al., 2000; Pessoa, 2008; Zelazo and Müller, 2002). This suggests the possibility that if an association between physiological and behavioral self-monitoring exists, it may be modulated by emotional context. Considering this point, three conditions that differed in the type of visual stimulus were included in the behavioral monitoring task (Fig. 1). One condition presented geometric figures (“object” condition), while the other two conditions used images of human faces that expresses disgust or happiness (“disgust-face” and “happy-face” conditions, respectively). These conditions were adopted based on studies demonstrating that neural activity during simple visuomotor tasks can be influenced by task-irrelevant visual stimuli that contain socio-emotional information, such as what is found in facial expressions (Boksem et al., 2011; Casey et al. 2011). For example, Casey et al. (2011) used fMRI to show that the task-irrelevant emotional expression of face stimuli altered the pattern of cortical activation, and magnified the individual differences that were observed during self-regulation tasks. Based on these previous reports, we chose to manipulate the emotional context during performance monitoring (i.e. Simon task). In particular, the disgust-face condition was imperative to this study. Disgust is believed to have originated from a basic survival function for detecting body abnormalities and expelling noxious objects (Angyal, 1941; Rozin et al., 2008). As such, it is one of the emotions most related to bodily internal states and interoceptive processing (Craig, 2003; Harrison et al., 2010; Phillips et al., 1997). We supposed that faces expressing disgust would more strongly activate interoceptive processing, which in turn would affect overlapping behavior-monitoring processes, and lead to higher correlations between physiological and behavioral monitoring during the disgust condition. The happy-face condition was added to examine the selectivity of emotional influence. We presumed four possible relationships between error processing and interoception: (1) no association in any stimulus condition, (2) a similar association irrespective of conditions, (3) an association only in emotional contexts (particularly in the disgust-face condition), and (4) associations in all the conditions, but particularly strong ones in emotional contexts (especially in the disgust-face condition). If the third or fourth case were true, the result would suggest some flexibility or context-dependency in the interaction between physiological and behavioral self-monitoring.

The primary aim of this study was therefore to determine whether an association between physiological monitoring and behavioral monitoring exists. To this end, we used separate tasks to assess each type of self-monitoring. The HCT was used to assess sensitivity of physiological monitoring. A set of stimulus–response compatibility tasks (Simon tasks; Simon and Rudell, 1967) were used to assess behavioral monitoring, and included conditions that manipulated emotional context. Electroencephalograms (EEGs) were acquired while subjects performed these tasks, and ERN and Pe components were used for analysis that

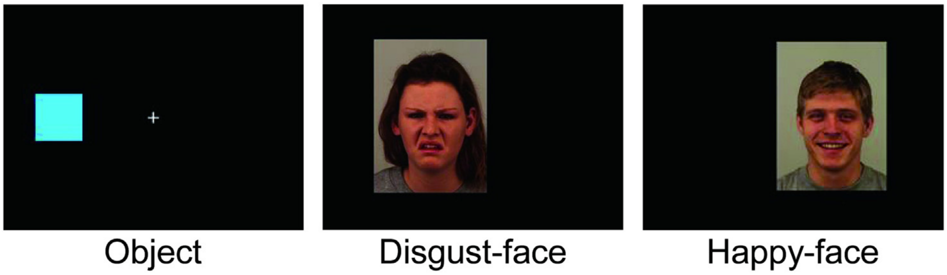

Fig. 1. Examples of the stimuli presented in each condition of the Simon task. *Left*, the object condition; *Center*, the disgust-face condition; *Right*, the happy-face condition. Note that the fixation point was occluded by foreground stimuli for the disgust-face and happy-face conditions.

focused on within-subject correlations between the measures obtained from the two tasks. As an index of behavioral adjustment, post-error slowing of RTs (i.e. the phenomenon that RT tends to be longer in a trial immediately after an error commission) as well as overall accuracy was also obtained (Danielmeier and Ullsperger, 2011). Cardiac activities were also measured to assess the arousal states of participants. We had two hypotheses. First, that HCT score would be correlated with the behavioral measures and magnitude of ERP responses elicited by the Simon tasks. In particular, association with HCT score would be higher for Pe amplitude than for ERN amplitude because the former reflects error awareness, which has been suggested to be related with interoceptive awareness. Second, any association between HCT score and ERP amplitudes would be greatest in the disgust-face condition because that particular emotion is related to interoceptive bodily processing.

2. Materials and methods

2.1. Participants

Twenty subjects (15 females) between the ages of 18 and 28 years (mean ± SD: 20.15 ± 2.15) participated in this study. All but one participant were right-handed. Participants were paid 1000 yen (approximately $10) for their participation and all gave their written informed consent before the experiments. The study was approved by the Kwansei Gakuin University (KGU) Research Ethics Review Board under the KGU Regulations for Research with Human Participants.

2.2. Heartbeat counting task (HCT)

During the experiment, participants were seated in a dimly lit, electrically shielded sound-attenuation room. While electrocardiograms (ECGs) were recorded (see below), participants were asked to count their own heartbeats during designated periods, and to verbally report the number of beats at the end of each trial. The start and finish of the designated periods were signaled acoustically. Following a practice trial, the experiment was conducted with three trials of different lengths (25 s, 40 s, and 60 s). The sequence of trials was randomized for each participant. The accuracy of heartbeat detection was calculated by comparing the counted heartbeats with the actual number of heartbeats (based on the ECG) with the following formula (Herbert et al., 2007):

$$\text{HCT score} = \frac{1}{3}\sum\left(\frac{1-|\mathit{recorded\,heartbeats}-\mathit{counted\,heartbeats}|}{\mathit{recorded\,heartbeats}}\right)$$

This equation yields the degree to which the number of subjective heartbeats matches that of actual heartbeats; when the two are equal, the score is 1 (maximum), and when no heartbeat is perceived, the score is 0 (lowest). An HCT score was calculated for each trial, and the final HCT score for each individual was the average score of the three trials.

2.3. Simon task

In the same experimental room, participants were seated ~1 m in front of a 19-inch CRT display. The Simon tasks were conducted with three conditions (object, disgust-face, and happy-face; Fig. 1). In the object condition, yellow or blue squares (visual angle of 3.3° × 3.3°) were presented either left or right of a white fixation cross (0.8° × 0.8°) centered on a black background. Participants were required to respond to a blue object by pressing a right button with their right thumbs, and to a yellow object by pressing a left button with left thumbs. Target stimuli in the disgust-face and happy-face conditions were male or female faces that were selected from the Karolinska Directed Emotional Faces database (Goeleven et al., 2008). Face stimuli (7.6° × 10.2°) were presented either on the right or left side of the fixation point. Participants were instructed to respond to male faces using their left thumbs and to female faces using their right ones.

In all conditions, a trial began with a fixation point centered on the display for 1000 ± 200 ms, followed by a target stimulus that was terminated by the participant's response. If the participant made an erroneous response, a feedback message ("ERROR!") was presented on the monitor for 1500 ms. If the participant failed to respond to a stimulus within 500 ms, the stimulus was terminated and a warning message ("Hurry up!") was presented for 1500 ms. Stimuli appeared on either the same side of the display as the required response (congruent trial) or on the opposite side (incongruent trial), with equal probability. Participants completed at least 3 blocks of 80 trials, and blocks were added until at least 20 error trials per condition were obtained for each participant. The three conditions were counter-balanced across participants.

2.4. Electrophysiological recording and analysis

While participants performed the Simon tasks, EEGs was recorded from Ag/AgCl electrodes located at Fp1, Fp2, Fz, FCz, F3, F4, F7, F8, FC3, FC4, FT7, FT8, Cz, C3, C4, T7, T8, TP7, TP8, CPz, CP3, CP4, Pz, P3, P4, P7, P8, Oz, O1, O2, A1, and A2. A ground electrode was placed at AFz and referred to an electrode affixed at the nose. EEGs were sampled at 1000 Hz with 0.1–100 Hz bandpass filter. ECGs were recorded from electrodes on the left and right wrists with the same sampling rate. In offline analysis, a 30-Hz low-pass filter was reapplied and EEGs were re-referenced to the averaged earlobe electrodes (A1/A2). All EEG data were segmented into 800-ms epochs based on the timing of responses, including a 200-ms pre-response baseline period. Segments in the three conditions were averaged separately for correct and error trials. Because the EEG montage did not involve vertical electrooculography, we chose to remove ocular and other motion artifacts using the threshold approach rather than a mathematical subtraction approach. Only segments within ± 150 μV in each channel were analyzed and baseline-corrected.

Error-related components were extracted from the ERPs obtained in error trials. To quantify ERN amplitudes, negative peaks with latencies ranging from 0 to 200 ms were detected in the waveforms averaged across error trials in each individual at FCz (where the ERN showed maximal amplitude on the grand-averaged waveform). Then the mean amplitude of a 10-ms time window centered on the negative peak was calculated. Pe amplitudes were calculated as the mean amplitudes in the period 300–400 ms post-response at Cz (where the grand-averaged component showed its maximum). Mean values ± SDs of averaged EEG epochs for the error trials were 15 ± 7.9, 23 ± 15.3, and 22 ± 15.1 for the object, disgust-face, and happy-face conditions, respectively. Although these numbers may not seem large, it has been shown that ERN amplitudes can be properly assessed by averaging as few as six trials (Olvet and Hajcak, 2009).

Heart rate (HR) and heart rate variety (HRV) in the Simon tasks were measured from the ECG data. Because the durations of task blocks were not long (approximately 2–3 min for each), we used the Lorenz-plot approach of HRV quantification; the Cardiac Vagal Index (CVI) was calculated as an estimate of parasympathetic influence to HRV, and the Cardiac Sympathetic Index (CSI) as an estimate of sympathetic influence (Toichi et al., 1997). Each cardiac measure was calculated for each block, and then averaged for each of the three conditions.

2.5. Statistical analysis

We determined whether each measure (ERP, behavioral, and cardiac) correlated with the HDR scores using two-sided Pearson's correlations. All p-values were corrected for multiple comparisons by controlling the false discovery rate (FDR) (Benjamini and Hochberg, 1995), separately for each component and other variables, with $\alpha = 0.05$.

3. Results

3.1. Behavioral measures

The mean score of the HCT was 0.68 ± 0.19 (range: 0.36–0.97), and no gender-based differences were found (males: 0.70; females: 0.67; $t(19) < 1, p = 0.782$).[1] Reaction times (RTs) in the Simon task for correct responses in the object, disgust-face, and happy-face conditions are shown in Table 1. A repeated-measures analysis of variance (ANOVA) was applied to the data with two within-subject factors: congruency (congruent or incongruent) and condition (object, disgust-face, or happy-face), revealing a significant main effect of congruency ($F_{(2,\ 38)} = 34.7$, $p < 0.001$). Another two-way ANOVA with factors of condition and preceding trial (post-correct or post-error; referring to trials following correct and erroneous responses, respectively) revealed a main effect of preceding trial ($F_{(1,\ 20)} = 183.77$, $p < 0.001$). Post-hoc analysis showed significant differences between all conditions ($ps < 0.001$), indicating that RTs in post-error trials were longer, regardless of stimulus condition. A main effect of condition was also found ($F_{(2,\ 40)} = 32.06$, $p < 0.001$). Post-hoc analysis showed RTs for objects were significantly faster than for either type of face ($ps < 0.001$), while RTs for faces did not differ depending on the emotional expression ($p = 0.90$). Correlation analysis revealed that RTs for post-correct trials, but not those for post-error trials, were positively correlated with HCT score (Table 1). Differences between post-error and post-correct trials that manifest in the magnitude of post-error slowing (Danielmeier and Ullsperger, 2011; Rabbitt, 1966) were also tested. This measure showed a negative correlation with HCT score in the object condition (Table 1).

Performance accuracy on the Simon tasks was also tested with a one-way ANOVA. This test revealed a significant main effect of condition ($F_{(2,\ 40)} = 17.99$, $p < 0.001$). Post-hoc analysis revealed that the object condition was easier than either of the face conditions ($ps < 0.001$), while performance on the face conditions did not differ from each other ($p = 0.75$). Additionally, HCT score tended to positively correlate with accuracy in the disgust-face condition ($r = 0.48$, $p = 0.096$), but not the other conditions (Table 1).

3.2. Cardiac measures

HR and two measures of HRV (CSV and CSI) in each condition of the Simon tasks are presented in Table 2. The one-way ANOVA revealed that there was no effect of condition either on HR ($F_{(2,\ 40)} = 0.96$, $p = 0.39$) and CSI ($F_{(2,\ 40)} = 1.56$, $p = 0.22$). A marginal main effect of condition was detected in CVI ($F_{(2,\ 40)} = 3.09$, $p = 0.057$); post-hoc analysis showed CVI in the disgust condition was lower than the object condition ($p = 0.024$). Correlation analysis showed that no index was related with the HCT score in all the conditions (Table 2).

3.3. ERPs

The amplitudes of ERN and Pe components elicited by the Simon tasks were calculated for each condition (Fig. 2 and Table 3). A one-way ANOVA showed no main effect of condition on ERN or Pe amplitudes (both $Fs_{(2,\ 40)} < 1$).

Regarding the correlation between the magnitudes of ERPs and interoceptive sensitivity, HCT score was found to be positively related to the ERN component in the disgust-face condition ($r = -0.67$, $p = 0.003$), but not in the other conditions. In contrast, Pe amplitude was positively correlated with HCT score in all three conditions (Table 3). There was a possibility that these correlations could be accounted in terms of individual difference of arousal or vigilance level. Therefore we applied partial correlation analysis on HCT and ERN/Pe amplitude by removing three variables (HR, CVI, and CSI) that reflect activity in the autonomic nervous system (i.e. peripheral arousal) in each condition. The resulting partial correlation coefficients are listed in Table 3 (see also Fig. 3). The results indicated that the combinations of significant correlation between ERPs and HCT score reported above were preserved and the associations were not likely to be attributed to general arousal.

There was another possibility that the correlations between ERPs and HCT score could be explained by task difficulty, considering that the behavioral results suggested that Simon-task difficulty varied across conditions. Therefore we further conducted partial correlation analysis by removing two parameters that could reflect task difficulty (mean RT and accuracy rate) in each condition. The resulting partial correlation coefficients for each condition were displayed in Table 3. Again, the results showed that the patterns of correlation between ERPs and HCT score were preserved, indicating that the associations were not due to behavioral performance.

4. Discussion

This study investigated how physiological monitoring (cardiac sensitivity) and behavioral monitoring (error processing) relate to each other by examining correlations between HCT score and the ERP magnitudes and behavioral measures obtained from the Simon tasks. Results showed that Pe amplitudes and RTs from all stimulus conditions were significantly correlated with HCT score. Additionally, HCT score correlated with ERN amplitude and behavioral accuracy only in the disgust-face condition.

4.1. ERP results

Regardless of the stimulus, HCT score was found to be robustly correlated with Pe amplitude, which is the later portion of error-related ERP responses. In contrast, association of HCT with the earlier ERN amplitudes did depend on the stimulus. Cardiac measures as well as

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[1] Like the HCT score, gender-based differences were not found for any other measure in this study. Generally, gender effects should not be ignored when examining bodily processes (Pennebaker and Roberts, 1992). In fact, it is known that males tend to be better at interoceptive tasks, including heartbeat perception (e.g., Katkin et al., 1981; Pennebaker and Roberts, 1992). Thus it should be noted that the statistically null results concerning gender difference in this study may be due to the skewed ratio of males to females.

Table 1
Behavioral results and their correlations with the heartbeat perception score.

	RT (post-correct)		RT (post-error)		RT (post-error vs. correct)		Accuracy	
	Mean (SD)	Pearson's *r*	Mean (SD)	Pearson's *r*	Mean (SD)	Pearson's *r*	Mean (SD)	Pearson's *r*
Object	330.6 (17.5)	0.49*	370.1 (15.9)	−0.05	39.56 (16.43)	−0.57*	85.0 (7.8)	0.25
Disgust face	357.9 (22.3)	0.48*	387.2 (21.9)	0.32	29.25 (12.89)	−0.31	76.7 (11.6)	0.48†
Happy face	359.0 (24.7)	0.43†	394.9 (21.2)	0.25	35.91 (15.87)	−0.34	77.2 (6.9)	0.22

Note that FDR correction for multiple testing was applied for each measure, and thus the same number of correlation coefficients can yield different probabilities.

† $p < 0.1$.

* $p < 0.05$.

behavioral data indicated that the associations between ERPs and HCT score were not likely to be accounted for by mere arousal or vigilance level. The stable association between HCT performance and Pe amplitudes supports our primary hypothesis that physiological monitoring and behavioral monitoring are substantially connected.

Several functional roles for ERN and Pe have been proposed, and although a clear consensus has not been achieved, their timing is widely agreed to reflect earlier (ERN) and later (Pe) stages of information processing after committing errors (Nieuwenhuis et al., 2001; Overbeek et al., 2005). A recent influential model of Pe function raised the possibility that it represents an accumulation of evidence that signals error commission (Steinhauser and Yeung, 2010; Ullsperger et al., 2010). This includes gathering information from internal as well as external cues to determine whether a recent action was an error. Taking this into account, the correlation between cardiac perception and Pe amplitude suggests that internal error signals may be perceived with higher saliency by individuals with higher sensitivity to their heartbeats.

Furthermore, it is thought that the accumulation of evidence that indicates errors leads to subjective awareness of error (Klein et al., 2013; Ullsperger et al., 2010). Importantly, reports have repeatedly demonstrated that compared with the ERN, Pe amplitude more strongly reflects the degree of error awareness (Endrass et al., 2007, 2005; Murphy et al., 2012; Nieuwenhuis et al., 2001; Overbeek et al., 2005; Shalgi et al., 2009). Therefore we can attribute the linkage between HCT score and Pe to the degree of conscious processing (i.e. awareness) for the two kinds of self-monitoring. Indeed, some researchers have argued that the coupling between the two domains is a way for the interoceptive signal to become an important cue that leads to subjective awareness of error commission (Hajcak et al., 2003; Ullsperger et al., 2010). Although error awareness was not explicitly measured here, our results may indirectly indicate such a linkage.

ERN amplitude was found to be correlated with HCT score only in the disgust-face condition. This result was consistent with our prediction that the association between interoceptive processing and error processing would be enhanced in this condition. Considering that a similar correlation was not found in the happy-face condition, the results cannot easily be attributed to emotional stimuli *per se*. Rather, they more likely reflect a selective effect of disgust. The disgust-face condition was primarily considered to induce negative affect that is often characterized by physical sensations. Disgust is thought to have originated as a negative response to the bad taste or smell of potentially harmful objects and is essentially associated with the detection of bodily abnormalities (i.e. an interoceptive process) (Angyal, 1941; Rozin et al., 2008). Thus, the disgust-face condition likely strengthened processing of physiological sensations in our subjects. Consequently, in the disgust-face condition, individual differences in interoceptive awareness were reflected not only in the later higher-level process (Pe) but also in the early automatic one (ERN). We interpret this to indicate some flexibility in the inter-domain linkage. The extent that behavioral monitoring relies on physiological monitoring could depend on the situation, and the emotional context is likely a factor that can modulate this interaction. This notion is in line with the prevailing view that emotion is deeply coupled with bodily states (Damásio, 1994; James, 1884).

Unexpectedly, ERN amplitude was significantly lower in the disgust-face condition. Intuitively, one may think that individuals with high interoceptive sensitivity would perceive internal cues of erroneous responses with higher saliency, leading to higher ERN amplitudes. In fact, a study has demonstrated enhanced ERNs with a Simon task that used disgust-face stimuli (Boksem et al., 2011). Why ERN amplitude was lower in the disgust condition of this study remains unexplained, although some studies suggest that there are minor differences among cultures in facial expression (Jack et al., 2012). Thus, racial mismatching of the models in the face-stimuli to the participants is one possible factor that may have influenced the results.

Another concern relates to the potential for our feedback to contaminate the ERP signals. We inserted feedback to increase the number of errors, and some feedback-related negativity (FRN; Miltner et al., 1997) might have become mixed in with the stimulus-evoked response. However, even if this occurred, we argue that the effect would be very limited in extent. FRNs are generated when feedback stimuli are the only means by which the result of an action can be known (e.g., Miltner et al., 1997; Gehring and Willoughby, 2002). We assume that this was not the case in our experiment, in which outcomes during the Simon task were realized at the moment responses were given (without feedback), a fact supported by the generation of ERNs at the moment responses were made. As feedback immediately after error commission has already been established as acceptable in some circumstances (Christ et al., 2000), and because feedback presentation was totally identical across conditions, we think that this issue did not have a significant impact on our findings.

4.2. Behavioral and physiological results

As was the case for ERP results, behavioral measures obtained from the Simon tasks provided both stimulus-independent and stimulus-dependent correlations with cardiac sensitivity. For all stimulus conditions, RTs correlated with HCT score in trials after correct responses, but not after erroneous ones. Good cardiac perceivers tended to show slower RTs in post-correct trials, indicating that RT was associated with interoceptive sensitivity when performances were not affected

Table 2
Cardiac measures and their correlations with the heartbeat perception score.

	HR		HRV-CVI		HRV-CSI	
	Mean (SD)	Pearson's *r*	Mean (SD)	Pearson's *r*	Mean (SD)	Pearson's *r*
Object	70.96 (10.48)	−0.24	4.30 (0.45)	−0.19	2.12 (0.76)	0.01
Disgust face	70.47 (10.81)	−0.15	4.24 (0.45)	−0.22	1.98 (0.69)	0.01
Happy face	70.07 (10.55)	−0.13	4.28 (0.46)	−0.14	1.97 (0.69)	0.08

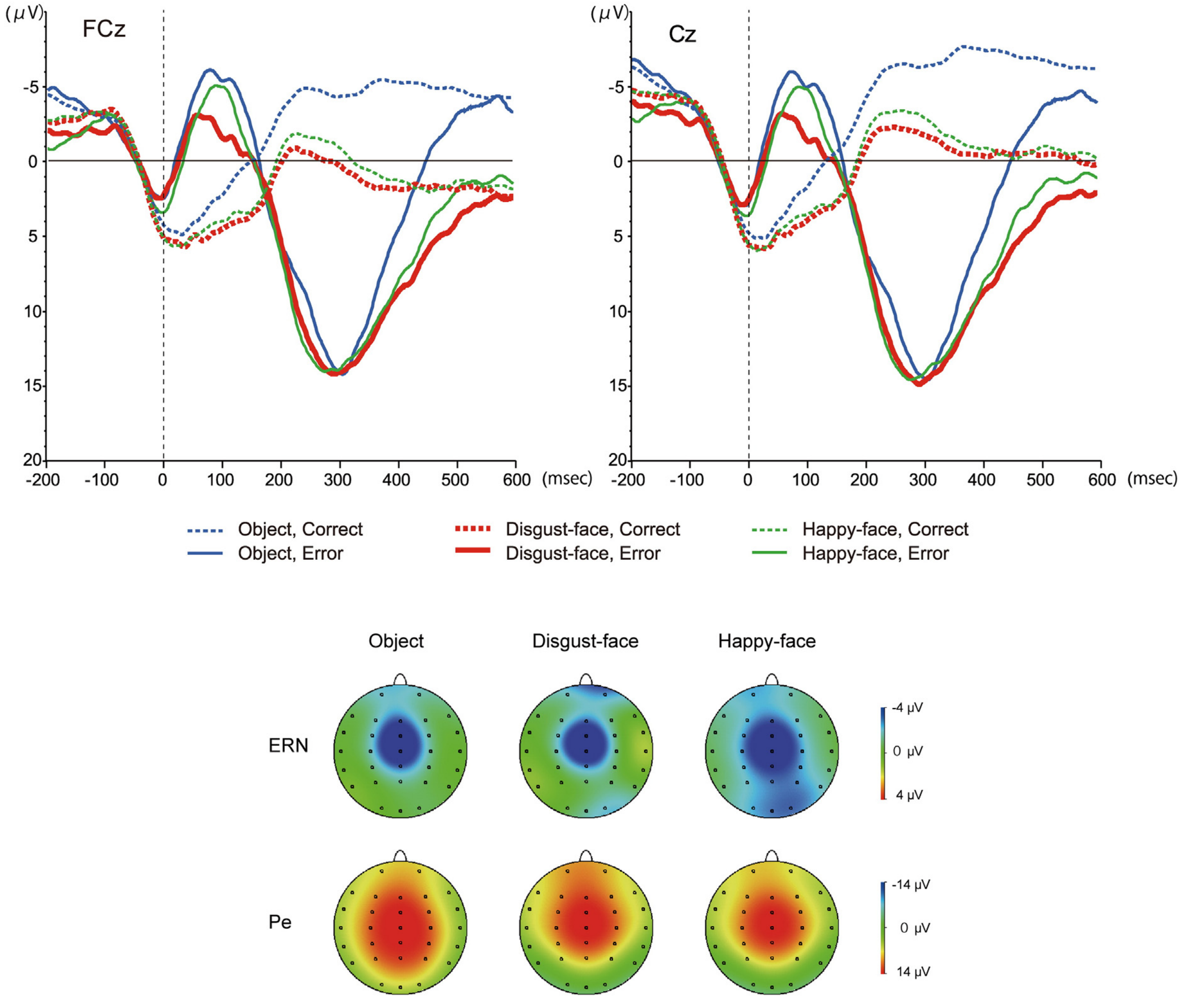

Fig. 2. Grand-averaged response-locked ERP waveforms and scalp distributions for each condition of the Simon task. In the waveforms at FCz and Cz, ERNs (negative peaks around 50–100 ms) and Pes (positive deflections after ~300 ms) were observed. Topographies of ERN and Pes at their respective peak latencies are shown viewed from the top with the nose pointing upward.

by a preceding error. A number of previous reports regarding post-error behavioral adjustments have demonstrated that RT is prolonged in trials immediately following an error response (called "post-error slowing"; Danielmeier and Ullsperger, 2011; Rabbitt, 1966) and this effect is accompanied by awareness of the error (Nieuwenhuis et al., 2001; Wessel et al., 2011). By this logic, the HCT score (interoceptive sensitivity) should have been related to the post-error RTs rather than the post-correct ones. As another way of estimating post-error slowing, the difference between post-error and post-correct RTs negatively correlated with HCT score in the object condition. We consider this correlation to be owing to the correlation in the post-correct trials mentioned above, and thus also difficult to interpret. A possible factor causing this unexpected result may be a temporal parameter of the task. We gave performance feedback after erroneous responses, but not after correct ones, so that time between a response and the next stimulus was different between post-error and post-correct trials. Some studies have shown that the degree of post-error slowing is significantly affected by the duration of response–stimulus interval (Danielmeier and Ullsperger, 2011; Jentzsch and Dudschig, 2009). Thus, the difference in timing could have contributed to the RT results obtained here. Aside from the RT results, the performance (percent correct) on the Simon tasks was found to marginally correlate with HCT score only in the disgust-face condition. As with the correlation between the ERN and HCT score, this result suggests an enhanced association

Table 3
ERP Amplitudes and their correlations with the heartbeat perception score.

	ERN				Pe			
	Mean (SD)	Pearson's r	Partial col. #1	Partial col. #2	Mean (SD)	Pearson's r	Partial col. #1	Partial col. #2
Object	−12.98 (7.98)	−0.44	−0.37	−0.31	18.93 (7.30)	0.60*	0.59*	0.70*
Disgust face	−10.91 (3.76)	−0.67*	−0.65*	−0.69*	18.33 (8.83)	0.55*	0.59*	0.53*
Happy face	−11.90 (5.44)	−0.33	−0.37	−0.33	18.07 (7.47)	0.51*	0.48*	0.49*

Partial col. #1 represents coefficients of partial correlation with the HCT with three cardiac measures (HR, CVI, and CSI) as control variables. Partial col. #2 represents those controlling behavioral measures (mean RT and accuracy).

* $p < 0.05$.

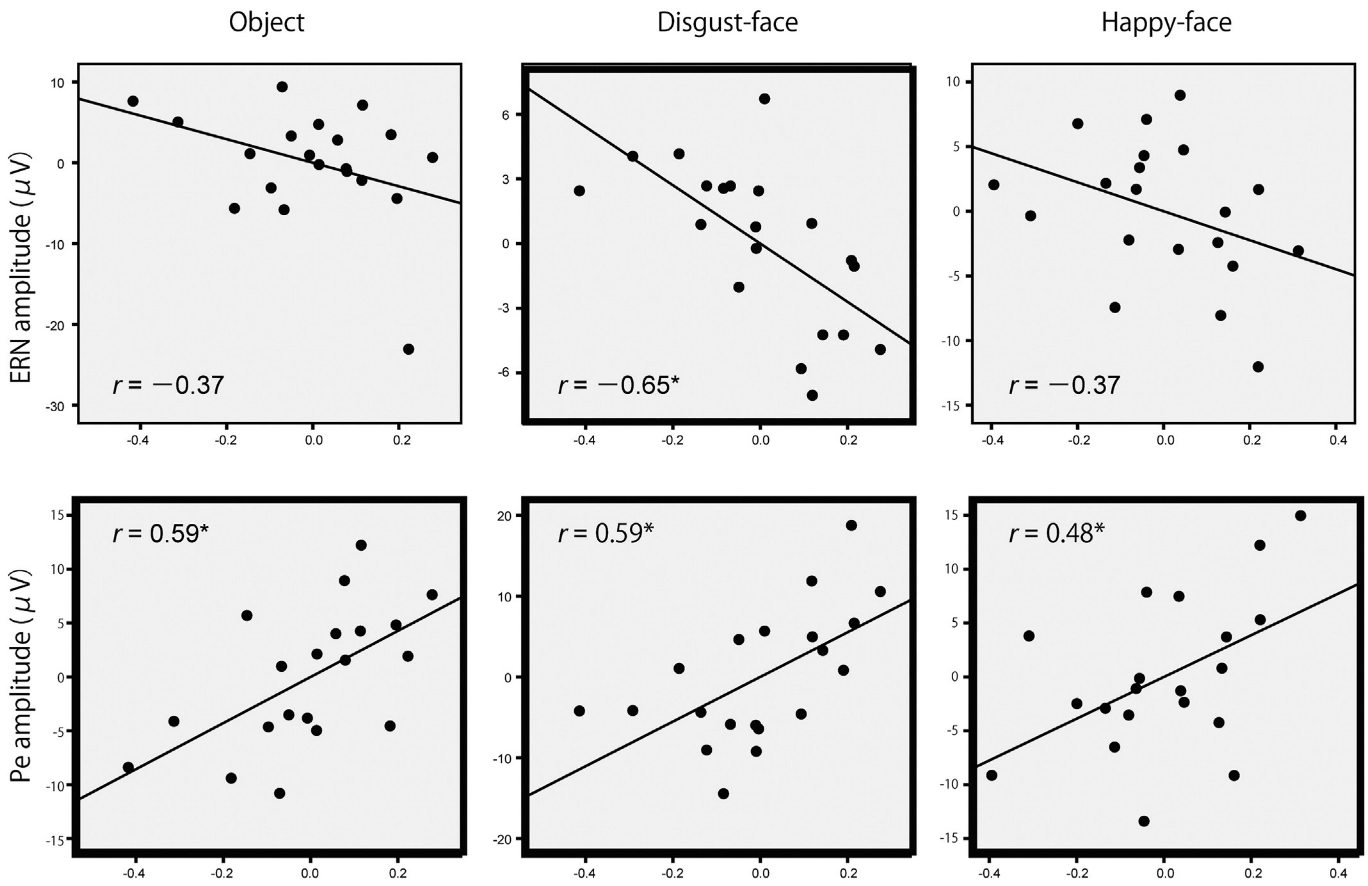

Fig. 3. Partial correlation plots of ERN and Pe amplitudes against HCT score. The effects of HR and two HRV measures (CVI and SCI) were removed in each condition. The ordinates of upper panels indicate ERN amplitudes and those of lower panels indicate Pe amplitudes. The abscissas of all panels represent the HCT score. All values are standardized in the calculation. Plots with significant correlations are indicated by a bold border.

between the two kinds of self-monitoring in the body-related emotional context.

Interpreting these behavioral results is not easy because of the limited number of studies showing covariance between cardiac perception and behavioral performance in a sensorimotor task. In a rare example, Matthias et al. (2009) examined the relation between interoceptive sensitivity and performance in a set of visual attention tasks. They found that compared with low HCT scores, those with high scores showed better performance in selective and divided attention tasks. As for RTs, they reported no difference between good and poor heartbeat perceivers. Together with their study, our behavioral results at least suggest that interoceptive awareness may be somewhat related to behavioral control in visuomotor tasks. However, this issue needs to be further examined before any definitive conclusions can be reached.

Regarding the physiological measures, HR and CSI (cardiac sympathetic index) did not differ across conditions. CVI (cardiac vagal index), which approximates respiratory sinus arrhythmia and is assumed to reflect parasympathetic activity (Toichi et al. 1997), decreased in the disgust-face condition. This result partially supports the idea that disgust is related to bodily processing, although it remains unclear whether the decrease in parasympathetic activity was caused by the specific emotion of disgust or by a general negative valence. Importantly, the change in CVI suggests that although the emotions expressed by the stimuli were irrelevant to the tasks, they still influenced the participants' nervous systems. However, as stated above, no measures of cardiac activity correlated with ERP amplitudes or HCT score. Thus, the ERP results indicate that the affective context (i.e. disgust-face condition) altered the way bodily and behavioral self-monitoring processes interact at the level of the central nervous system, and these results were not likely because of peripheral physiology or general arousal.

4.3. Possible neural substrates for the present findings

Although the present study did not investigate the exact brain areas that contribute to the two tasks, studies on interoception and error processing have described brain areas related to each function independently. These studies show that ACC and AIC are associated with both types of self-monitoring (e.g. Critchley et al., 2004; Debener et al., 2005; Hester et al., 2005). When interpreting the present findings, we give particular weight to AIC because other studies have suggested several points that relate this region to the present study. First, Pe amplitude that was robustly correlated with heartbeat perception score in this study, has been suggested to be associated with AIC activity (Klein et al., 2007; Ullsperger et al., 2010). Second, the feeling of disgust, which was a context that enhanced the coupling of physiological and behavioral monitoring, is considered to be centered in the insula region including AIC (Harrison et al., 2010; Phillips et al., 1997). Third, conscious experiences of internal process are thought to be associated with the AIC, in both physiological monitoring (interoceptive awareness) and behavioral monitoring (error awareness) (e.g. Craig, 2009; Hester et al., 2005; Klein et al., 2013; Pollatos et al., 2007a). Although we did not explicitly measure conscious processes in behavioral monitoring, we regard awareness as a shared factor that might influence the degree of sensitivity for both domains of self-monitoring. Taking these points together, we speculate that AIC is a hub that connects multiple types of internal monitoring.

4.4. Limitations of this study and future directions

This study has a few limitations. First, awareness of erroneous responses was not measured. Error awareness may be an important factor influencing the association between interoceptive awareness and error processing, but without this measure we cannot directly address that issue here. Second, additional negative emotions (such as anger or sadness) were not used. Doing so in future studies will allow us to clarify whether the enhanced correlation between behavioral monitoring and cardiac sensitivity was due specifically to the feeling of disgust, or whether it can be elicited with any type of negative affect. Third, based on the significant differences in task performance among conditions, we have to admit that the present study failed to control task difficulty. This factor possibly confounded neural activity related to error processing (Masaki et al., 2007; Pailing and Segalowitz, 2004), and may have affected the association between physiological sensitivity and task performance on the Simon task. The main findings here are common across conditions, indicating that this issue should not affect the interpretation of the data. However, a future study should control task performance to further clarify the nature of the ERN/Pe responses found here.

Finally, we would like to note the usefulness of our underlying approach to investigate the contribution of processing bodily sensations to different cognitive domains. For example, studies with this approach have shown that interoception and emotional self-reflection activate common brain regions (Terasawa et al., 2013), and that both interoception and performance monitoring have some association with social cognition, such as empathy to others (Fukushima and Hiraki, 2009; Fukushima et al., 2011). The current approach can be expected to extend to other types of self-monitoring, such as mental introspection or evaluation of the social state of the self, in attempts to further clarify the nature of the multiple layers of selfhood.

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