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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