Neural Systems Connecting Interoceptive Awareness and Feelings

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Abstract: In many theories of emotions the representations of bodily responses play an important role for subjective feelings. We tested the hypothesis that the perception of bodily states is positively related to the experienced intensity of feelings as well as to the activity of first-order and second-order brain structures involved in the processing of feelings. Using a heartbeat perception task, subjects were separated into groups with either high or poor interoceptive awareness. During emotional picture presentation we measured high-density EEG and used spatiotemporal current density reconstruction to identify regions involved in both interoceptive awareness and emotion processing. We observed a positive relation between interoceptive awareness and the experienced intensity of emotions. Furthermore, the P300 amplitudes to pleasant and unpleasant pictures were enhanced for subjects with high interoceptive awareness. The source reconstruction revealed that interoceptive awareness is related to an enhanced activation in both first-order structures (insula, somatosensory cortices) and second-order structures (anterior cingulate, prefrontal cortices). We conclude that the perception of bodily states is a crucial determinant for the processing and the subjective experience of feelings. *Hum Brain Mapp 28:9–18, 2007.* © **2006 Wiley-Liss, Inc.**

Key words: evoked potentials; emotions; electroencephalography; heartbeat perception; visceral sensation; insula; anterior cingulate; prefrontal cortex; somatosensory cortex

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INTRODUCTION

During imagination of an affective situation, for example, being desperately in love or frightened to death, most people report strong bodily sensations accompanying their feelings. This observation led William James [1884] to postulate that viscero-afferent feedback is closely linked to emotional experience, and furthermore, that feelings originate from the perception of these bodily changes. In short, we feel emotions because we perceive our bodily reactions [see Bennett and Hacker, 2005]. For producing an emotion James suggested three essential steps. An emotional stimulus initiates particular visceral, vascular, or somatic activities; for example, changes of blood pressure and heart rate. Therefore,

different emotional states should be characterized by differential bodily states. Until now, this assumption was discussed rather controversially, with several authors claiming that such a specificity of response does not exist, starting with Cannon's famous response on James [Cannon, 1927; see also Bradley, 2000]. Nevertheless, this hypothesis could be confirmed by many studies using visual emotional stimuli [Collet et al., 1997; Critchley et al., 2005; Dimberg et al., 2000; Levenson et al., 1990; Surakka and Hietanen, 1998]. In a recent publication, Critchley et al. [2005] demonstrated that the level of brain activity in interconnected brain regions including amygdala, insula, anterior cingulate, and brainstem predict the observed degree of heart rate increase to emotional facial expressions.

While James' view has been under investigation until today and continues to be a topic of debate [Barbalet, 1999; Bennett and Hacker, 2005; Critchley et al., 2004, 2005; Ellsworth, 1994; Lang, 1995; Reisenzein, 1983], the idea that the perception of bodily signals is an essential component in the constitution of feelings has found its way into modern neuropsychological theories of emotions. One important theoretical approach in which perception of bodily changes plays

an essential role is the somatic marker theory of Damasio [1994, 1999; Bechara and Naqvi, 2004]. Damasio sharply distinguishes between three stages of emotion processing: "a state of emotion, which can be triggered and executed nonconsciously; a state of feeling, which can be represented nonconsciously; and a state of feeling made conscious, i.e., known to the organism having both emotion and feeling" [Damasio, 2000, p. 37]. It is stated that an emotional object, either derived from the environment or recalled from memory, causes activation in so-called emotion trigger sites (ventromedial prefrontal cortex, amygdala, brain stem nuclei, hypothalamus, and basal forebrain) which induce changes toward the body and other brain regions. Both the organism with its ongoing visceral sensations, as well as the object with its interactions to sensory and motor structures are mapped as neural patterns in so-called first-order mapping structures (e.g., insula, somatosensory cortices). Feelings are based on both the activity of the described first-order structures as well as on the activity of so-called second-order structures (cingulate, thalamus, brainstem nuclei, hypothalamus, and basal forebrain) representing "the pattern of the object, the pattern of the organism and the relationship between object and organism" [Damasio, 2000, p. 194].

Damasio's model is confirmed by research data showing that the described anatomical structures (insular cortex, somatosensory cortices, cingulum, thalamus, prefrontal cortex) are direct or indirect recipients of signals from the internal milieu and the viscera [Cameron, 2001, 2002; Critchley et al., 2002, 2004; Phan et al., 2002; Pollatos et al., 2005]. The importance of first-order and second-order structures for the feeling of emotions was demonstrated by imaging data: Damasio et al. [2000] found that during the feeling of different self-generated emotions both first-order mapping structures like the somatosensory cortices and the insula as well as second-order structures like the cingulated cortex and nuclei in the brainstem were activated. Lane et al. [1998] showed that the activity in the anterior cingulate was crucial for the accurate detection of emotional signals that were perceived either interoceptively or exteroceptively. Also, Beauregard et al. [2001] demonstrated that conscious self-regulation of emotion involved the right prefrontal cortex and the right anterior cingulate. As James postulated, feelings originate from the perception of bodily changes. When considering the theories of James and Damasio together, feelings as well as the perception of bodily changes should be reflected in the activity of certain brain structures (first- and second-order structures). One would conclude that differences in the ability to perceive bodily changes are reflected in the experience of emotions and in the activity of first-order structures (insula, somatosensory cortices) and second-order structures (cingulate, thalamus, brainstem, hypothalamus, and prefrontal cortex).

In terms of investigating the relationship between the perception of bodily states and feelings by means of behavioral data, there are few studies that have found the postulated positive relationship between interoceptive awareness and emotional experience [Ferguson and Katkin, 1996; Han-tas et al., 1984; Montoya and Schandry, 1994; Schandry, 1981; Wiens et al., 2000]. Using visual stimuli, Wiens et al. [2000] reported a positive relationship between the experienced intensity of emotions and the perception of bodily changes as measured by a heartbeat perception task. Following Damasio's model, the Jamesian postulation that feelings originate from the perception of bodily changes must be reflected in an analogous relation between interoceptive awareness and the activity in first- and second-order structures as specified in the somatic marker theory. To our knowledge, no study exists so far that addressed this question by investigating both subjective feelings and brain processes in relation to the perception of bodily states.

The goal of the present study was to test the hypothesis that the perception of bodily states is positively related to both the experienced intensity of feelings as well as to the activity of first- and second-order brain structures involved in the processing of emotional stimuli. Brain processes involved in the processing of emotional stimuli can be studied by means of event-related potentials (ERPs). In numerous ERP studies affective pictures have been used as emotional stimulus material [Carretie et al., 1997; Cuthbert et al., 2000; Keil et al., 2002; Palomba et al., 1997; Waldstein et al., 2000]. In all studies mentioned, a greater response was observed in the P300 amplitude to pictures with emotional content as compared to neutral ones. P300 is very sensitive to higher-order aspects of perceptual and central information processing [Hamm et al., 2003; Katayama and Polich, 1998; Kok, 1996, 1997; Polich and Kok, 1995; Spencer et al,, 2001]. P300 is also related to the experienced intensity of feelings, as late positive potentials (P300, slow wave) were found to be enhanced for pleasant and unpleasant pictures that subjects rated as more intense than other pictures of the same affective categories [Cuthbert et al., 2000; Hamm et al., 2003]. Therefore, P300 is a suitable ERP component for investigating the addressed hypothesis. Concerning the hypothesized engagement and the activity of certain brain structures in emotion processing, the source reconstruction method is one approach to locate cortical generators of P300 elicited by emotional pictures. Since multichannel measurements contain not only temporal, but also spatial information, spatiotemporal coupled current density reconstruction (stCDR) can be used to identify potential sources of evoked brain potentials [Darvas et al., 2001; Schmitt et al., 2001; Waberski et al., 2001]. Waberski et al. [2001] showed that the generators of the mismatch negativity can be assessed by means of spatiotemporal source imaging on the basis of 64-channel electroencephalography data. They focused on the time course and localization of proposed frontal sources of the mismatch negativity and found additional generators within the anterior cingulate gyrus and the inferior temporal gyrus that were clearly separated from the supratemporal generators in space and time course. In a recent study, Esslen et al. [2004] used multichannel EEG to identify relevant brain areas and the time-course of emotional processing. First they identified time segments of significant differences between responses to emotional and neutral faces, and for these

significant segments statistical analyses of functional low-resolution electromagnetic tomography (LORETA) images were performed. Esslen et al. [2004] found significant differences within the first 500 ms after stimulus onset, with the strongest activation found in the happy, sad, and disgust conditions in extended frontotemporal areas. It is now an interesting question whether by the use of spatiotemporal coupled current density reconstruction (stCDR) brain regions engaged in both interoceptive awareness can be identified.

In order to assess the perception of bodily changes, the most extensively studied interoceptive process is heartbeat perception [Cameron, 2001]. The ability to detect one's heartbeats accurately can be measured by different heartbeat detection tasks and is often equated with interoceptive ability or interoceptive awareness in general [Crtichley et al., 2004; Katkin et al., 2001; Leopold and Schandry, 2001; Montoya et al., 1993; Pollatos and Schandry, 2004; Wiens et al., 2000]. One common observation is the existence of substantial, interindividual differences in heartbeat perception. According to the performance in heartbeat perception tasks, subjects are often classified as good vs. poor heartbeat perceivers and therefore as either having high or poor interoceptive awareness, respectively [Katkin et al., 2001; Pollatos and Schandry, 2004; Pollatos et al., 2005; Wiens et al., 2000]. The ability to perceive cardiac activity may depend on such factors as gender, percentage of body fat, and physical fitness [Cameron, 2001; Jones, 1994]. Significant differences in heartbeat perception ability were also observed in different clinical samples: Mussgay et al. [1999] demonstrated a tendency toward lower perception scores in patients with depressive, somatoform, and personality disorders, whereas Ehlers et al. [1992, 2000] reported more accurate heartbeat perception in panic patients. Patients suffering from arrhythmias and benign palpitations [Ehlers et al., 2000] and patients with diabetic neuropathy [Leopold and Schandry, 2001] showed a decreased heartbeat perception ability compared with healthy controls. Thus, differences in heartbeat perception are of clinical relevance and seem to be a suitable tool for assessing the perception of bodily changes.

As stated above, the present study aimed to test the hypothesis that interoceptive awareness is positively related to both the experienced intensity of feelings as well as to the activity of first- and second-order brain structures involved in the processing of emotional stimuli. We examined in detail whether subjects with high interoceptive awareness report a greater intensity of feelings evoked by emotional pictures. Also, we hypothesized that subjects with high interoceptive awareness show enhanced P300 amplitude elicited by emotional pictures. Furthermore, subjects with high interoceptive awareness should show an enhanced activity in first-order (insula, somatosensory cortices) and second-order structures (cingulate, thalamus, brainstem, hypothalamus, and prefrontal cortex) as identified by source reconstruction during the P300 time window.

SUBJECTS AND METHODS

Subjects

The sample consisted of 32 students (16 male) from the University of Munich. Subjects received €30 (about $36) for their participation. The mean age was 25.3 (standard deviation [SD], 4.5) years ranging from 18–36 years of age.

Stimulus Material

Sixty pictures chosen from the International Affective Picture System [Center for the Psychophysiological Study of Emotion and Attention, 1999] served as emotional stimuli. According to the normative ratings of the IAPS [Center for the Psychophysiological Study of Emotion and Attention, 1999], there were 20 pleasant, 20 neutral, and 20 unpleasant pictures. This number of stimuli was chosen according to a former EEG study [Pollatos et al., 2003] that revealed good practicability and a sufficient signal-to noise ratio in most subjects. Pleasant, neutral, and unpleasant slides differed significantly regarding valence (means, 7.4, 5.0, and 3.0, respectively; F(2,57) = 311.8; $P < 0.001$). Neutral pictures were significantly less arousing (mean, 2.8; F(2,57) = 83.30; $P < 0.001$) than both pleasant (mean, 5.5) and unpleasant (mean, 5.9) slides. Emotional slides were projected on a screen at a distance of 1.9 m from the subjects' eyes. The visible size of the pictures was 75 × 50 cm, resulting in a picture presentation with a visual angle of 22° horizontally and 15° vertically. Luminance did not differ significantly between valence categories (F(2,57) = 0.655, P = n.s.).

Procedure

After attachment of the electrodes, cap electrode positions and anatomical landmarks (nasion, right/left preauricular points) were measured using a Zebris digitizer system. First, interoceptive awareness was assessed using 11 heartbeat-counting phases (varying in length) in accordance with the Mental Tracking Method suggested by Schandry [1981]. Participants were asked to count their own heartbeats silently and to verbally report the number of counted heartbeats at the end of the counting phase. The beginning and the end of the counting intervals were signaled acoustically. Interoceptive awareness was estimated as the mean heartbeat perception score according to the following transformation:

1/11 Σ (1 – (|recorded heartbeats–counted

heartbeats|)/recorded heartbeats)

The mean obtained heartbeat perception score was 0.77 (SD 0.20). Sixteen subjects (10 female) with a score above 0.85 (mean [SD], 0.92 [0.04]) were assigned to the group with high interoceptive awareness. These subjects were contrasted with 16 subjects with low interoceptive awareness (mean [SD], 0.62 [0.17]). There were no significant differences concerning gender and age between interoceptive awareness groups.

The picture presentation began with a short training procedure, after which 60 pictures were shown in a randomized order. A single trial always began with a fixation cross followed by an IAPS slide visible for 6 s. Subjects were instructed to avoid exploratory eye-movements and eye-blinks and to attentively watch the pictures. Immediately after slide offset the subjects were asked to provide valence and arousal ratings on a 9-point scale using a paper and pencil form of the Self Assessment Manikin (SAM) [Bradley and Lang, 1994]. The SAM is a nonverbal pictorial assessment technique that directly measures the valence and arousal associated with a person's affective reaction to a wide variety of stimuli. The rating interval lasted 15 s. The whole experimental procedure had a duration of ~40 min.

Analysis of the Self-Reported Feelings

Mean valence and arousal ratings were calculated separately for the three emotion contents (pleasant, unpleasant, and neutral) and submitted to repeated measures analyses of variance (ANOVAs) with three levels of emotion content and two levels of interoceptive awareness (high/low).

EEG Recording

EEG activity was recorded from 62 leads with a DC amplifier (bandpass: 0.01–100 Hz; SYNAMPS, Neuroscan) and digitized at a sampling rate of 250 Hz. Electrode positions were determined with an electrode cap (Falk Minow Services, Herrsching, Germany). The reference electrode was positioned at the tip of the nose; the ground electrode was placed on the left cheek. Offline, EEG was re-referenced to linked mastoids.

Horizontal and vertical eye movements were recorded with electrodes placed at the outer canthus of each eye (EOG_H) and above and below the left eye (EOG_V). Nonpolarizable Ag-AgCl electrodes were used. Electrode resistance was maintained below 5 K°.

ECG Recording

The ECG was measured through nonpolarizable Ag-AgCl electrodes attached to the right mid clavicle and lower left rib cage. ECG activity was recorded analogous to the EEG (bandpass: 0.01–100 Hz). R-waves were detected online and were stored on a separate trigger channel.

Data Reduction and Analysis

The EEG record was examined for EOG, muscle activity, and other sources of electrophysiological artifact. Blinks were corrected using the Gratton et al. [1983] algorithm implemented in the analysis software (Vision Analyser). Trials that were contaminated by artifacts were eliminated prior to averaging, accounting for approximately 6% of the trials (neutral condition: 5%, positive condition: 7%, negative condition: 7%). The EEG was filtered (bandpass 0.01–30 Hz) and averaged offline. EEG sweeps were triggered by the onset of the slide presentation. Sampling epochs extended from 100 ms prior to the trigger onset to 900 ms after trigger onset.

Visually evoked potentials were averaged for 12 regions, formed by crossing hemisphere (right/left) with horizontal plane (anterior, medial, posterior), and vertical plane (inferior, superior; see Fig. 4). Mean voltages were assessed in the time window of P300 (290–500 ms). The data were analyzed using ANOVAs with two levels of hemisphere (right/left), six levels of region (anteroinferior, anterosuperior, medial-inferior, medial-superior, posteroinferior, posterosuperior), three levels of emotion content (pleasant, unpleasant, and neutral), and two levels of interoceptive awareness (high/low interoceptive awareness). Where appropriate, degrees of freedom were adjusted after Greenhouse and Geisser. In the Results section, uncorrected F-values are reported together with the Greenhouse-Geisser epsilon values and corrected probability levels.

Current Density Reconstruction

Current density reconstruction was calculated using the software package EaSI (Electro-anatomical Source Imaging, Brain Products, München, Germany). Within this software the representation of a normal brain is implemented in the form of the T1-weighted structural MR provided by the Montreal Neurological Institute. A finite element model was used with the gray matter serving as the source space with a regular grid normalized to the AC-PC line resulting in 1,650 possible source locations. Individually measured positions of the electrodes were mapped onto the surface of the template T1 image using four landmarks (nasion, inion, left and right preauricular points). For reconstruction of current density the spatiotemporal coupled linear Minimum-Norm was used [Darvas et al., 2001] leading to a spatially as well as a temporally smoothed distribution. The following steps for localizing the main generators of P300 were applied independently to the waveforms of each subject.

(1) First, the current density reconstruction was performed for each individual dataset for the entire time range from 0–900 ms. A time window from –100 ms to 0 ms served as a noise estimate. In contrast to the statistical analyses of ERP data, the source reconstruction was based on data for each condition and each subject derived from the original (unpooled) 62 leads. For sources reconstruction the LORETA algorithm [Pascual-Marqui and Biscay-Lirio, 1993] was applied using the L2-Norm with temporal coupling [Darvas et al., 2001]. The regularization values λ and μ were calculated automatically. Time source series were stored separately for each subject and each condition and standardized by dividing them by their maximum activity.

(2) Specification of clusters of sources followed the implemented cluster algorithm [Darvas, 2001]. First, the strength of each source at each possible location was computed and the local maxima for each point in the specified time range was determined. Then for each

subject a matrix representing the distances between all maxima was computed. Finally, all clusters with a distance of less than 30 mm were combined into one cluster.

(3) Clusters were computed for the time range from 290–500 ms (P300) resulting in the mean location for different clusters and the mean source magnitude within a cluster.

(4) Only clusters that were identified in at least 50% of the subjects in one awareness group in each condition were admitted to further analysis to reduce possible influence of noise on the results. Additionally, clusters were selected only if their strength accounted for at least 50% of the individual maximum source strength. This procedure provided clusters of activation expected to contribute significantly to P300.

(5) For the P300 time window, the standardized activation values were submitted to a mixed design ANOVA with the repeated measures Hemisphere (left, right), Emotional Content (positive, negative, neutral), and Interoceptive Awareness (high, low awareness). In the case of significant main or interaction effects, post-hoc analyses were performed in order to examine in which emotion content differences between subjects with high and poor interoceptive awareness occurred.

The specified clusters were anatomically specified by means of Talairach and Tournoux coordinates using the Talairach demon software (http://ric.uthscsa.edu/projects/registration). Figure 3 illustrates the obtained clusters in each interoceptive awareness group for the P300 time window separately for each emotion content. For P300 a total of five main clusters could be identified based on the described grand averages, roughly corresponding to the anterior cingulate (BA 32/10; Coordinates 6, 37, 25), the prefrontal cortex (BA 6/8 ; Coordinates 6, 7, 66), the somatosensory cortex (BA 7/40; Coordinates 4, −60, 52), the right insula (BA 13; Coordinates 33, 17, 6), and the visual cortices (BA 18/19; Coordinates −49, −75, −9; 55, −73, −15).

RESULTS

Experienced Feelings during Emotional Picture Presentation

Figure 1 shows the valence and arousal ratings for all three experimental conditions separated for subjects with high and poor interoceptive awareness.

With respect to *arousal ratings*, a highly significant main effect of Arousal ($F(2,60) = 188.1$; $P < 0.001$; $\eta^2 = 0.86$; $\epsilon = 1.0$) was assessed. Pleasant and unpleasant pictures were rated as more intense than neutral ones ($P < 0.05$). The between-subject factor Interoceptive Awareness ($F(1,30) = 4.85$; $P < 0.05$; $\eta^2 = 0.14$; $\epsilon = 0.57$), as well as the interaction between Emotion Content (pleasant, neutral, unpleasant pictures) and Interoceptive Awareness ($F(2,60) = 4.02$; $P < 0.05$; $\eta^2 = 0.12$; $\epsilon = 0.70$) were significant,
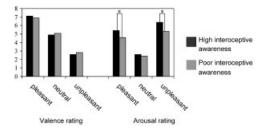

Figure 1.
Mean valence and arousal scores for subjects with high (n = 16) and poor (n = 16) interoceptive awareness (*P < 0.05).

indicating that subjects with high interoceptive awareness reported more intense feelings toward pleasant (mean, 5.4 vs. 4.6; $F(1,30) = 4.2$; $P < 0.05$; $\eta^2 = 0.12$; $\epsilon = 0.51$) and unpleasant pictures (mean, 6.4 vs. 5.3; $F(1,30) = 9.57$; $P < 0.01$; $\eta^2 = 0.24$; $\epsilon = 0.85$), while no differences occurred for neutral slides (mean, 2.6 vs. 2.4; $F(1,30) = 0.17$; $P = $ n.s.).

With respect to *valence ratings*, the statistical analysis revealed a highly significant effect for Emotion Content ($F(2,60) = 224.58$; $P < 0.001$; $\eta^2 = 0.88$; $\epsilon = 1.00$). Post-hoc Bonferroni-adjusted analyses revealed that valence ratings for pleasant pictures (mean, 6.9) were significantly higher as compared to neutral (mean, 5.0; $P < 0.001$) and unpleasant slides (mean, 2.8; $P < 0.001$). In addition, valence ratings for neutral slides were significantly higher as compared to unpleasant slides ($P < 0.001$). Neither the between-subject factor Interoceptive Awareness was significant ($F(1,30) = 0.20$; $P = $ n.s.), nor the interaction effect between Emotion Content and Interoceptive Awareness ($F(2,60) = 0.60$; $P = $ n.s.).

Visual Evoked Potentials to Emotional Pictures

As can be seen in Figure 2, the course of the visual evoked potentials differed between subjects with high and low interoceptive awareness in the latency ranges later than 250 ms.

In accordance with the latency ranges reported in earlier studies using emotional pictures as stimuli [Cuthbert et al., 2000; Keilet al., 2000; Palomba et al., 1997], P300 (mean amplitude 290–500 ms) was examined in more detail.

Statistical Analyses of the Visual Evoked Potentials

In the P300 latency range, a main effect of Interoceptive Awareness ($F(1,30) = 6.03$, $P < 0.01$; $\eta^2 = 0.17$, $\epsilon = 0.66$) was assessed: Subjects with high interoceptive awareness revealed higher amplitudes (4.47 µV) than subjects with low interoceptive awareness (2.98 µV). Post-hoc repeated measurement ANOVAs for each emotion content revealed significant differences, depending on interoceptive awareness for pleasant and unpleasant pictures. For pleasant pictures, subjects with high interoceptive awareness showed significantly higher activation in the anterior-superior (3.71 µV vs. 0.76 µV; $F(1,30) = 5.33$, $P < 0.05$, $\eta^2 = 0.15$, $\epsilon = 0.61$) and
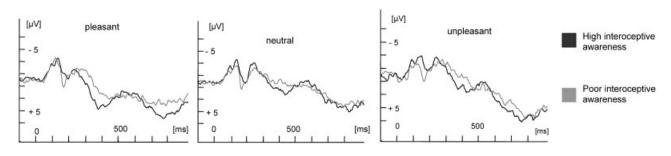
Figure 2.
Visual evoked potentials to pleasant, neutral, and unpleasant pictures for subjects with high (n = 16)
and poor (n = 16) interoceptive awareness (at F3).

medial-superior region (7.18 µV vs. 3.78 µV; F(1,30) = 8.12, $P < 0.01$, $\eta^2 = 0.21$, $\epsilon = 0.79$). For unpleasant pictures, subjects with high interoceptive awareness again showed significantly higher activation over the medial-superior region (5.40 µV vs. 3.43 µV; F(1,30) = 6.03, $P < 0.05$, $\eta^2 = 0.17$, $\epsilon = 0.66$).

Current Density Reconstruction

Based on the described current density reconstruction (see Subjects and Methods), five main activation clusters could be located for P300. These clusters were roughly corresponded to the anterior cingulate (BA 32/10), the prefrontal cortex (BA 6/8), the somatosensory cortices (BA 7/40), the right insula (BA 13), and the visual cortices (BA 18/19). Figure 3 displays the current densities for subjects with high and subjects with poor interoceptive awareness based on the grand averages of both interoceptive awareness groups. As clearly shown in Figure 3, there were substantial differences between both interoceptive awareness groups, showing overall differences in activation strength concerning the observed clusters.

The statistical analyses based on the individually obtained datasets are summarized in Table I. Subjects with high interoceptive awareness had an overall higher activation level in the prefrontal cortex and the somatosensory cortices. In the anterior cingulate, subjects with high interoceptive awareness yielded higher activation scores only for pleasant and unpleasant pictures, whereas in the right insula this effect was limited to unpleasant stimuli. Interoceptive awareness had no significant effect on the activation of the visual cortices.

DISCUSSION

The goal of the present study was to test the hypothesis that the perception of bodily states is positively related to both the experienced intensity of feelings as well as to the activity of first- and second-order brain structures involved in the processing of emotional stimuli.

One main result we found was that subjects with high interoceptive awareness reported more intense feelings while viewing pleasant and unpleasant pictures. This result is in accordance with the Jamesian postulation that feelings
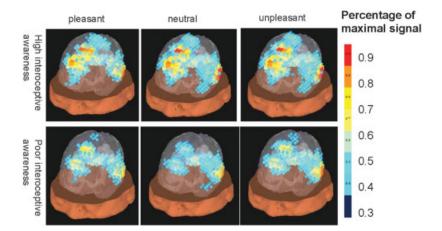

Figure 3.
Source reconstruction for subjects with high (n = 16) and poor (n = 16) interoceptive awareness
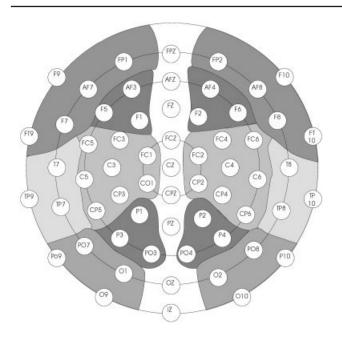in the P300 latency range (492 ms).

Figure 4.
Forming of 12 electrode pools (anteroinferior, anterosuperior, medial-inferior, medial-superior, posteroinferior, posterosuperior).

originate from the perception of bodily changes. One can conclude that subjects who habitually perceive their bodily states with higher accuracy experience feelings as more intense because they detect bodily changes in response to emotional stimuli with higher accuracy than subjects with poor interoceptive awareness. This assumption is confirmed by other studies demonstrating that interoceptive awareness is correlated with emotional experience on the level of verbal reports [Blascovich et al., 1992; Critchley et al., 2004; Ferguson and Katkin, 1996; Hantas et al., 1982; Leopold and Schandry, 2001] or on the level of behavioral data [Wiens et al., 2000].

Our data extend these research results, as we show that subjects with high interoceptive awareness not only report a greater experienced intensity of feelings, but also show an enhanced P300 amplitude to pleasant and unpleasant stimuli that is reflected in a greater activity of both first-order mapping structures (right insula, somatosensory cortices) as well as second-order mapping structures (anterior cingulate, prefrontal cortex) serving as main generators of the P300 response to emotional stimuli. P300 can be seen as a classical brain electrical indicator of emotional arousal [Carretie et al., 1997; Cuthbert et al., 2000; Keil et al., 2002; Palomba et al., 1997], known to be enhanced for pictures that are rated as more emotionally intense [Cuthbert et al., 2002]. Thus, the observed enhanced P300 amplitude in the high interoceptive awareness groups for pleasant and unpleasant stimuli can be interpreted as a modulation reflecting simultaneous differences in emotional intensity.

Concerning the observed brain structures underlying P300 as identified by spatiotemporal Current Source Density Reconstruction, our data is in accordance with other studies showing that dipoles in the frontal, occipital, and parietal cortices serve as main generators of P300 [Anderer et al., 2003; Goto et al., 1996; Pascual-Marqui et al., 1998; Tarkka et al., 1996; Yamazaki et al., 2001]. In a recent study [Esslen et al., 2004], visual evoked potentials to emotional faces were examined within the first 500 ms after stimulus onset using LORETA to identify relevant brain areas and to describe the time course of emotion processing. Esslen et al. [2004] found for each emotional condition specific activation patterns in different brain regions including the anterior cingulate, prefrontal, temporal, and subcortical brain regions. Their results are highly congruent with the observed activation in the present study where emotional pictures were presented and activation was modeled for a time range of 290–500 ms after stimulus onset.

Interoceptive awareness had a great impact on the observed psychophysiological reaction to emotional stimuli: We found activation differences in relation to interoceptive awareness both in first-order mapping structures like the

TABLE I. Regions with enhanced activation in subjects with high interoceptive awareness during the P300 latency range

	Prefrontal cortices (BA 6/9)	Anterior cingulate (BA 32/10)	Somatosensory cortices (BA 7/40)	Insula (BA 13)	Visual cortices (BA 18/19)
Activation					
Pleasant	86%	69%	78%	53%	84%
Neutral	83%	69%	69%	40%	90%
Unpleasant	90%	66%	81%	62%	87%
Effect of interoceptive awareness	$*F(1,30) = 4.99$	$*F(1,30) = 4.58$	$**F(1,30) = 8.79$	$*F(1,30) = 5.10$	n.s.
Post-hoc analyses					
Pleasant	$*F(1,30) = 7.25$	$**F(1,30) = 8.01$	$*F(1,30) = 5.25$	n.s.	n.s.
Neutral	$*F(1,30) = 7.28$	n.s.	$*F(1,30) = 4.86$	n.s.	n.s.
Unpleasant	$*F(1,30) = 5.26$	$*F(1,30) = 6.99$	$**F(1,30) = 8.65$	$**F(1,30) = 8.61$	n.s.

$*P < 0.05; **P < 0.01.$
n.s., not significant.

insula and the somatosensory cortices that contribute to the primary representation of bodily states, and in second-order mapping structures like the anterior cingulate and parts of the prefrontal cortex that contribute to the experience-dependent remapping of bodily states [Critchley et al., 2001; Damasio, 1999]. The first-order structures (insula, somatosensory cortices) as well as the second-order structures (anterior cingulate, prefrontal cortex) were found to be activated during the feeling of different emotions [Damasio et al., 2000], a finding corresponding to our data. Nevertheless, some questions remain open concerning the way in which to interpret these results. One possible explanation is that interoceptive awareness is related to a greater sensitivity to emotional signals, leading to a greater response in first-order mapping structures and/or a larger physiological response, and subsequently to a greater activation of second-order mapping structures. As Damasio stated, the disposition to respond to emotional stimuli somatically in a certain way is the product of social learning, "connecting specific classes of stimuli with specific classes of somatic state" [Damasio, 1994, p. 177]. Interoceptive awareness may facilitate this learning process by using so-called somatic markers more precisely due to an increased accuracy in the detection of bodily changes. This interpretation is confirmed by data from Katkin et al. [2001], who showed that the perception of visceral cues facilitated the prediction of shocks in a conditioning task.

As far as the somatosensory cortices are concerned, the general representation for the body seems to be enhanced in subjects with high interoceptive awareness, as the observed activation differences were present for all picture contents. This result might reflect the general attention allocated toward one's body, which is larger in subjects with high interoceptive awareness. This is an interpretation confirmed by data showing a higher activation in the somatosensory cortices in good heartbeat perceivers when focusing the attention on one's heartbeats [Critchley et al., 2004; Pollatos et al., 2005]. Concerning the activation of the right insula, we observed a congruent activation only during unpleasant picture presentation, where subjects with high interoceptive awareness produced a greater activation. The special importance of the insula for the processing of unpleasant stimuli is further confirmed by a recent functional MRI (fMRI) study [Critchley et al., 2004], demonstrating that anxiety correlated with the blood oxygen level-dependent (BOLD) response in the right insula. Also, the theoretical approach of Craig [2002, 2003] highlights the importance of the right insula for both emotion processing and interoceptive awareness, suggesting that this region translates visceral states into subjective feelings and self-awareness. Although there are many studies showing that heart rate changes are related to activation of the right insula [Augustine, 1996; Bennaroch, 1993; Cameron, 2001, 2002; Cechetto et al., 1990, Critchley et al., 2000, 2001; King et al., 1999; Williamson et al., 1999, 2002], it still remains an open question whether the observed higher activation in the described first-order mapping structures is accompanied by a greater bodily response pattern to emo-tional stimuli as measured by autonomic, visceral, and skeletomotor responses. Further research will need to be conducted in order to elucidate this question.

A very interesting result obtained was that interoceptive awareness was related to a greater activation of the anterior cingulate, a second-order structure, when viewing pleasant and unpleasant stimuli. The anterior cingulate is known to be involved in any form of attention that serves to regulate both cognitive and emotional processes [Phan et al., 2002]. In the present study, the anterior cingulate activation could represent the cognitive processes that are probably involved in the task. Concerning the importance of this structure for linking emotion processing with the perception of bodily states, Lane et al. [1998] showed that the activity in the anterior cingulate was related to the accurate detection of emotional signals. Also, Beauregard et al. [2001] demonstrated the engagement of the anterior cingulate in the conscious processing of emotional stimuli. Thus, a greater activation of the anterior cingulate in subjects with high interoceptive awareness may reflect a more sensitive detection of changes in bodily states occurring during emotions and feelings. Independent of whether interoceptive awareness is related to a greater physiological response to emotional stimuli, the anterior cingulate may serve as an interface structure for translating emotional reactions into differential somatic responses. A higher activation of this structure in subjects with high interoceptive awareness may lead to an enhanced somatic response to emotional stimuli which is then re-represented in first-order mapping structures like the insula and the somatosensory cortices. This interpretation is confirmed by Critchley et al. [2005], who showed that the anterior cingulate was one interface structure responsible for translating emotional reactions to facial expressions into differential cardiac responses. Among other brain structures, activity in the anterior cingulate predicted the observed heart rate increases to emotional facial expressions [Critchley et al., 2005].

The present study shows for the first time that the perception of bodily states is positively related to both the experienced intensity of feelings as well as to the activity of first-order and second-order brain structures involved in the processing of emotional stimuli. Thus, we provide evidence for the Jamesian postulation that feelings originate from the perception of bodily changes and identify certain brain regions that may serve as an interface between interoceptive awareness and feelings.

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REFERENCES

Anderer P, Pascual-Marqui RD, Semlitsch HV, Saletu B (1998): Electrical sources of P300 event-related brain potentials revealed

by low resolution electromagnetic tomography. Neuropsychobiology 37:20–27.

Anderer P, Saletu B, Semlitsch HV, Pascual-Marqui RD (2003): Non-invasive localization of P300 sources in normal aging and age-associated memory impairment. Neurobiol Aging 24:463–479.

Augustine JR (1996): Circuitry and functional aspects of the insular lobe in primates including humans. Brain Res Rev 22:229–244.

Barbalet JM (1999): William James' theory of emotions: filling in the picture. J Theory Soc Behav 29:251–266.

Beauregard M, Levesque J, Bourgouin P (2001): Neural correlates of conscious self-regulation of emotion. J Neurosci 21:1–6.

Bechara A, Naqvi N (2004): Listening to your heart: interoceptive awareness as a gateway to feeling. Nat Neurosci 7:102–103.

Bechara A, Damasio H, Damasio AR (2000): Emotion, decision making and the orbitofrontal cortex. Cereb Cortex 10:295–307.

Bennaroch EE (1993): The central autonomic network: functional organization, dysfunction, and perspective. Mayo Clin Proc 68:998–1001.

Bennett MR, Hacker PMS (2005): Emotion and cortical-subcortical function: conceptual developments. Prog Neurobiol 75:29–52.

Blascovich J, Brennan K, Tomaka J, Kelsey RM, Hughes P, Coad ML, Adlin R (1992): Affect intensity and cardiac arousal. J Pers Soc Psychol 63:164–174.

Bradley MM (2000): Emotion and motivation. In: Tassinary LG, Cacioppo JT, editors. Handbook of Psychophysiology. New York: Cambridge University Press. p 602–642.

Bradley MM, Lang PJ (1994): Measuring emotion: the self-assessment manikin and the semantic differential. J Behav Ther Exp Psychiatry 25:49–59.

Cameron OG (2001): Interoception: the inside story — a model for psychosomatic processes. Psychosom Med 63:697–710.

Cameron OG (2002): Visceral Sensory Neuroscience. Oxford: Oxford University Press.

Cannon WB (1987): The James-Lange theory of emotions: a critical examination and an alternative theory. By Walter B. Cannon, 1927. Am J Psychol 100:567–586.

Carretie L, Iglesias J, Garcia T (1997): A study on the emotional processing of visual stimuli through event-related potentials. Brain Cogn 34:207–217.

Cechetto DF, Saper CB, Yasui Y (1990): Cardiovascular area of the insular cortex and its efferent projections in the rat. Neurosci Res 15:23.

Center for the Psychophysiological Study of Emotion and Attention (1999): The international affective picture system (IAPS): technical manual and affective ratings. Gainesville, FL: NIMH-Center for the Study of Emotion and Attention, University of Florida.

Collet C, Vernet-Maury E, Delhomme G, Dittmar A (1997): Autonomic nervous system response patterns specifity to basic emotions. J Auton Nerv Syst 62:45–57.

Craig AD (2002): How do you feel? Interoception: the sense of the physiological condition of the body. Nat Rev Neurosci 3:655–666.

Craig AD (2003): Interoception: the sense of the physiological condition of the body. Curr Opin Neurobiol 13:500–505.

Critchley HD, Corfield DR, Chandler MP, Mathias CJ, Dolan RJ (2000): Cerebral correlates of autonomic cardiovascular arousal: a functional neuroimaging investigation in humans. J Physiol 523:259–270.

Critchley HD, Mathias CJ, Dolan R (2001): Neuroanatomical basis for first- and second-order representations of bodily states. Nat Neurosci 4:207–212.

Critchley HD, Wiens S, Rothstein P, Öhmann A, Dolan R (2004): Neural systems supporting interoceptive awareness. Nat Neurosci 7:189–195.

Critchley HD, Rotshtein P, Nagai Y, O'Doherty J, Mathias CJ, Dolan R (2005): Activity in the human brain predicting differential heart rate responses to emotional facial expressions. Neuroimage 24:751–762.

Cuthbert BN, Schupp HT, Bradley MM, Bierbaumer N, Lang PJ (2000): Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. Biol Psychol 52:95–111.

Damasio AR (1994): Descartes' Error: Emotion, Reason and the Human Brain. New York: Grosset/Putman.

Damasio AR (1999): The Feeling of What Happens: Body and Emotion in the Making of Consciousness. New York: Harcourt Brace.

Damasio AR, Grabowski TJ, Bechara A, Damasio H, Ponto LLB, Parvizi J, Hichwa RD (2000): Subcortical and cortical brain activity during the feeling of self-generated emotions. Nat Neurosci 3:1049–1056.

Darvas F, Schmitt U, Louis AK, Fuchs M, Knoll G, Buchner H (2001): Spatio-temporal current density reconstruction (stCDR) from EEG/MEG-data. Brain Topogr 13:195–207.

Dimberg U, Thunberg M, Elemehed K (2000): Unconscious facial reactions to emotional facial expressions. Psychol Sci 11:86–89.

Ehlers A, Margraf J, Roth WT (1992): Imipramine and alprazolam effects on stress test reactivity in panic disorder. Biol Psychiatry 31:35–51.

Ehlers A, Mayou R, Sprigings DC, Birkhead J (2000): Psychological and perceptual factors associated with arrhythmias and benign palpitations. Psychosom Med 62:693–702.

Ellsworth PC (1994): William James and emotion: is a century of fame worth a century of misunderstanding? Psychol Rev 101:222–229.

Esslen M, Pascual-Marqui RD, Hell D, Kochi K, Lehmann D (2004): Brain areas and time course of emotional processing. Neuroimage 21:1189–1203.

Ferguson ML, Katkin ES (1996): Visceral perception, anhedonia, and emotion. Biol Psychol 42:131–145.

Goto Y, Brigell MG, Parmeggiani L (1996): Dipole modeling of the visual evoked P300. J Psychosom Res 41:71–79.

Gratton G, Coles MGH, Donchin E (1983): A new method for off-line removal of ocular artefact. Electroencephalogr Clin Neurophysiol 55:468–484.

Hamm AO, Schupp HT, Weike AI (2003): Motivational organization of emotions: autonomic changes, cortical responses, and reflex modulation. In: Davidson RJ, Scherer K, Goldsmith HH, editors. Handbook of Affective Sciences. Oxford: Oxford University Press. p 187–211.

Hantas MN, Katkin ES, Blascovich J (1982): Relationship between heartbeat discrimination and subjective experience of affective state. Psychophysiology 19:563.

Hantas MN, Katkin ES, Reed SD (1984): Cerebral lateralization and heartbeat discrimination. Psychophysiology 21:274–278.

James W (1884): What is an emotion? Mind 9:188–205.

Katayama J, Polich J (1998): Stimulus context determines P3a and P3b. Psychophysiology 35:23–33.

Katkin E, Wiens S, Öhman A (2001): Nonconscious fear conditioning, visceral perception, and the development of gut feelings. Psychol Sci 12:366–370.

Keil A, Bradley M, Hauk O, Rockstroh B, Elbert T, Lang PJ (2002): Large-scale neural correlates of affective picture processing. Psychophysiology 39:641–649.

King AB, Menon RS, Hachinski V, Cechetto DF (1999): Human forebrain activation by visceral stimuli. J Comp Neurol 413:572–582.

Kok A (1996): On the utility of P3 amplitude as a measure of processing capacity. Psychophysiology 38:557–577.

Kok A (1997): Event-related-potentials reflections of mental resources: a review and synthesis. Biol Psychol 45:19–56.

Lane RD, Reiman EM, Axelrod B, Yun LS, Holmes A, Schwartz GE (1998): Neural correlates of emotional awareness: evidence of an interaction between emotion and attention in the anterior cingulated. J Cogn Neurosci 10:525–535.

Lang PJ (1995): The emotion probe. Studies of emotion and attention. Am Psychol 50:372–385.

Lang PJ, Bradley MM, Cuthbert BN (1997): Motivated attention: affect, activation, and action. In: Lang PJ, Simons RF, Balaban MT, editors. Attention and Orienting: Sensory and Motivational Processes. Hillsdale, NJ: Lawrence Erlbaum. p 97–135.

Leopold C, Schandry R (2001): The heartbeat-evoked brain potential in patients suffering from diabetic neuropathy and in healthy control persons. Clin Neurophysiol 112:674–682.

Levenson RW, Ekman P, Friesen WV (1990): Voluntary facial action generates emotion-specific autonomous nervous system activity. Psychophysiology 27:363–384.

Montoya P, Schandry R (1994): Emotional experience and heartbeat perception in patients with spinal cord injury and control subjects. J Psychophysiol 8:289–296.

Mussgay L, Klinkenberg N, Rueddel H (1999): Heart beat perception in patients with depressive, somatoform, and personality disorders. J Psychophysiol 13:27–36.

Palomba D, Angrilli A, Mini A (1997): Visual evoked potentials, heart rate responses and memory to emotional pictorial stimuli. Int J Psychophysiol 27:55–67.

Pascual-Marqui RD, Biscay-Lirio R (1993): Spatial resolution of neuronal generators based on EEG and MEG measurements. Int J Neurosci 68:93–105.

Phan KL, Wager T, Taylor, SF, Liberzon I (2002): Functional neuroanatomy of emotion activation studies in PET and fMRI. Neuroimage 16:331–348.

Polich J, Kok A (1995): Cognitive and biological determinants of P300: an integrative review. Biol Psychol 41:103–146.

Pollatos O, Schandry R (2004): Accuracy of heartbeat perception is reflected in the amplitude of the heartbeat-evoked brain potential. Psychophysiology 41:476–482.

Pollatos O, Kirsch W, Schandry R (2005): On the relationship between interoceptive awareness, emotional experience, and brain processes. Brain Res Cogn Brain Res 25:948–962.

Pollatos O, Kirsch W, Schandry R (2005): Brain structures involved in interoceptive awareness and cardioafferent signal processing. A dipole source localization study. Hum Brain Mapp 26:54–64.

Reisenzein R (1983): The Schachter theory of emotion: two decades later. Psychol Bull 94:239–264.

Schandry R (1981): Heart beat perception and emotional experience. Psychophysiology 18:483–488.

Schandry R, Sparrer B, Weitkunat R (1986): From the heart to the brain: a study of heartbeat contingent scalp potentials. Int J Neurosci 30:261–275.

Schmitt U, Louis AK, Darvas F, Buchner H, Fuchs M (2001): Numerical aspects of spatio-temporal current density reconstruction from EEG/MEG-data. IEEE Trans Med Imaging 20:314–324.

Spencer KM, Dien J, Donchin E (2001): Spatiotemporal analysis of the late ERP responses to deviant stimuli. Psychophysiology 38:343–358.

Stevens AA, Skudlarski P, Gatenby JC, Gore JC (2000): Event-related fMRI of auditory and visual oddball tasks. Magn Reson Imaging 18:495–502.

Surakka V, Hietanen JK (1998): Facial amd emotional reactions to Duchenne and non-Duchenne smiles. Int J Psychophysiol 29:23–33.

Talairach J, Tournoux P (1988): Co-planar Stereotactic Atlas of the Human Brain. New York: Thieme Medical.

Tarkka IM, Micheloyannis S, Stokic DS (1996): Generators for human P300 elicited by somatosensory stimuli using multiple dipole source analysis. Neuroscience 75:275–287.

Waberski TD, Kreitschmann-Andermahr I, Kawohl W, Darvas F, Ryang Y, Gobbele R, Buchner A (2001): Spatio-temporal source imaging reveals subcomponents of the human auditory mismatch negativity in the cingulum and the right inferior temporal gyrus. Neurosci Lett 308:107–110.

Waldstein SR, Kop WJ, Schmidt LA, Haufler AJ, Krantz DS, Fox NA (2000): Frontal electrocortical and cardiovascular reactivity during happiness and anger. Biol Psychol 55:3–23.

Whitehead WE, Drescher VM (1980): Perception of gastric contractions and self-control of gastric motility. Psychophysiology 17:552–558.

Wiens S, Mezzacappa ES, Katkin E (2000): Heartbeat detection and the experience of emotions. Cognit Emotion 14:417–427.

Williamson JW, McColl R, Mathews D, Ginsburg M, Mitchell JH (1999): Activation of the insular cortex is affected by the intensity of exercise. J Appl Physiol 87:1213–1219.

Williamson JW, McColl R, Mathews D, Mitchell JH, Raven PB, Morgan WP (2002): Brain activation by central command during actual and imagined handgrip under hypnosis. J Appl Physiol 92:1317–1324.

Winer BJ (1971): Statistical Principles of Experimental Design. New York: McGraw-Hill.

Yamazaki T, Kamijo K, Kiyuna T, Takaki Y, Kuroiwa Y (2001): Multiple dipole analysis of visual event-related potentials during oddball paradigm with silent counting. Brain Topogr 13:161–168.