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Interoceptive sensitivity and emotion processing: An EEG study ☆

Beate M. Herbert [a,b,*], Olga Pollatos [a], Rainer Schandry [a,1]

[a] Department of Psychology, Biological Psychology, Ludwig-Maximilians-University of Munich, Leopoldstr. 13, 80802 Munich, Germany
[b] Department of Clinical and Cognitive Neuroscience, University of Heidelberg, Central Institute of Mental Health, Mannheim, Square J5, 68159 Mannheim, Germany

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Abstract

Theories of emotion consider the self-perception of visceral activity to play an important role in emotion. This study examined the relationship between interoceptive sensitivity and both the subjective emotional experience and the processing of emotional pictures. According to their results in a heartbeat detection task subjects were classified as good ($N = 17$) or poor ($N = 20$) heartbeat perceivers. Event-related potentials were recorded while subjects viewed pleasant, neutral and unpleasant pictures and SAM ratings were examined. Good heartbeat perceivers showed significantly greater P300 and slow wave amplitudes for emotional pictures at antero-inferior, medial and posterior electrode sites and experienced a greater arousal for emotional pictures compared to poor heartbeat perceivers. The heartbeat perception score correlated significantly positive both with emotional P300 and slow wave amplitudes as well as with the arousal ratings for emotional pictures. The results indicate that there is a significant and strong association between interoceptive sensitivity and the intensity of emotional experience as well as the central processing of emotional stimuli.

Keywords: Interoceptive sensitivity; Heartbeat perception; Emotion; EEG; P300; Slow wave; Visual evoked potentials

1. Introduction

Many theories of emotion have postulated a close relationship between the self-perception of physiological signals and emotion processing: in an article published in Mind (1884) William James defined the experience of an emotion as the perception of bodily responses in the presence of emotional stimuli or imagination. In 1885 the physiologist Carl Lange proposed a similar theory (Lange, 1987). Since this time the so-called James–Lange theory of emotion has been almost continuously under debate and has been of great influence on theories of emotion (e.g. Cacioppo et al., 1992; Cameron, 2001; Craig, 2002; Critchley et al., 2004; Damasio, 1994, 1999; Lang, 1994; Reisenzein et al., 1995). Based on the Jamesian theory, Schachter and Singer (1962) proposed that bodily arousal must be perceived to trigger emotional experience. Schachter and Singer (1962) suggested that an emotion occurs when general physiological arousal is perceived, which is labelled cognitively according to contextual social cues.

A modern successor to the James–Lange theory of emotion, the somatic marker hypothesis of Antonio Damasio and co-workers (Bechara et al., 2000; Damasio, 1994, 1999), directly incorporates this view and emphasizes the importance of visceral and somatosensory feedback to enact emotion. According to this model, automatically generated bodily arousal responses induced by external or internal events feed back to the brain to guide motivational behavior (Damasio, 1994, 1999) and to influence emotional processing (Blair and Cipolotti, 2000; Damasio, 1994) as well as social cognition and decision making (Blair and Cipolotti, 2000; Bechara, 2004; Damasio, 1994).

Accounting for the fact that it might not be the mere occurrence of peripheral changes but the perception of physiological signals

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* Corresponding author. Department of Clinical and Cognitive Neuroscience, University of Heidelberg, Central Institute of Mental Health, Mannheim, Square J5, 68159 Mannheim, Germany. Tel.: +49 621 1703 3641; fax: +49 621 1703 6305.
E-mail addresses: beate.herbert@gmx.de (B.M. Herbert), schandry@psy.uni-muenchen.de (R. Schandry).
[1] Tel.: +49 89 2180 5176; fax: +49 89 2180 5233.

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that affects emotional experience (e.g. Katkin, 1985; Wiens et al., 2000; Wiens, 2005; Schandry, 1981), an important consequence arising from these theories is that a person's interoceptive sensitivity, varying widely among individuals (e.g. Cameron, 2001; Jones, 1994; Katkin, 1985; Leopold and Schandry, 2001; Schandry et al., 1993; Wiens et al., 2000), should influence subjective affective experience. Individuals who are highly sensitive to their visceral activity should demonstrate greater affective responses to emotion-laden stimuli than individuals who are less sensitive (e.g. Bechara, 2004; Craig, 2002; Damasio, 1994; Vaitl, 1996). There is ample evidence for such a positive relationship between the degree of a subject's visceral awareness and the subjective experience of emotions (e.g. Cameron, 2001; Critchley et al., 2004; Ferguson and Katkin, 1996; Hantas et al., 1982; Jones, 1994; Montoya and Schandry, 1994; Schandry, 1981; Wiens et al., 2000; Wiens and Palmer, 2001). In most cases heartbeat perception has been chosen to study interoceptive sensitivity. Cardiac activity is closely related to emotional experience, and the sensitivity to cardiac signals can be easily measured by heartbeat perception tasks (e.g. Brener and Kluvitse, 1988; Cameron, 2001; Critchley et al., 2004; Schandry, 1981; Wiens et al., 2000). For example, persons who could detect their heartbeats reported experiencing more intense emotions than poor detectors when viewing film clips targeting different emotions (Wiens et al., 2000). Furthermore, good and poor heartbeat perceivers did not differ significantly in physiological activity, such as heart rate and electrodermal activity (Wiens et al., 2000). A recent study by Barrett et al. (2004) demonstrated that good heartbeat perceivers showed more arousal focus than poor perceivers. The trait 'arousal focus' signals an individual's sensitivity to the implied degree of experiencing activation and deactivation of emotion words in describing emotional experiences in daily life.

Concerning the neural correlates of heartbeat detection there are convincing results, showing that good heartbeat perceivers demonstrate a greater cortical processing of signals from the cardiovascular system. Good heartbeat perceivers show a more pronounced heartbeat-evoked potential (HEP), a brain wave that appears contingent to the heartbeat over frontal and central electrodes, compared to poor heartbeat perceivers (Schandry et al., 1986; Pollatos and Schandry, 2004). This activity pattern has been shown to reflect sources in the anterior cingulate, the right insula, the prefrontal cortex, and the secondary somatosensory cortex with good heartbeat perceivers showing higher dipole strength than poor heartbeat perceivers in all four cortical sources (Pollatos et al., 2005a). These regions are also highly congruent with functional imaging data by Critchley et al. (2004) obtained during subjects concentrating their attention to their heartbeats. Recent results also demonstrated activation of the somatosensory, anterior and posterior cingulate cortices, the insula and brainstem nuclei during the feeling of self-generated emotions, suggesting that these structures monitor the internal emotional state of the organism (Damasio et al., 2000). Especially, the anterior cingulate cortex and the insula are suggested to play important roles for linking visceroception and emotion processing, as well as for the conscious perception of visceral signals (Craig, 2002; Critchley et al., 2004). Furthermore, all the mentioned brain structures are parts of a central network relevant for emotion processing and feelings (Craig, 2002; Damasio, 1994, 1999; LeDoux, 1996).

Summarizing the above mentioned concepts and findings, one arrives at the following conclusion: persons who are highly sensitive to internal bodily events should not only show an intensified subjective emotional experience during emotional stimulation but also an enhanced activity at the "level of brain processes" during the processing of emotional stimuli. Thus, our aim was to examine the relationship between emotional experience, as well as emotion processing and interoceptive sensitivity at the electrophysiological level. There is one study investigating this problem, however in an indirect manner. Based upon the reasoning that individual differences in the intensity of emotional experience reflect variation in sensitivity to internal bodily responses, Critchley et al. (2004) measured regional brain activity by fMRI during an interoceptive task wherein subjects judged the timing of their own heartbeats. The authors could demonstrate that in right insular/opercular cortex, neural activity predicted the subjects' accuracy in the heartbeat detection task as well as that local grey matter volume in the same region correlated with both interoceptive accuracy and subjective ratings of visceral awareness. Furthermore, indices of negative emotional experience correlated with interoceptive accuracy across subjects. Critchley et al. (2004) suggested that the right anterior insula supports a representation of visceral responses accessible to awareness, providing a substrate for subjective feeling states and linking awareness of visceral responses and subjective emotional experience.

In the present study we wanted to examine whether the extent of visceral sensitivity is not only related to the subjective emotional experience, but also to the processing of emotional stimuli. We used visual event-related brain potentials in order to investigate the processing of emotional pictures. Brain responses to the passive viewing of affective pictures have been studied frequently by using a variety of measures, including the event-related potential (e.g. Cacioppo and Gardner, 1999; Cuthbert et al., 2000; Keil et al., 2002; Palomba et al., 1997; Waldstein et al., 2000). A major finding of this research has been a modulation of late deflections of the ERP as a function of motivational significance (Keil et al., 2001, 2002; Lang et al., 1997). The response to emotionally salient (i.e. pleasant or unpleasant) compared to neutral pictures is characterized by a greater magnitude of the P300 deflection as well as a sustained later positivity (e.g. Cacioppo et al., 1994; Cuthbert et al., 2000; Keil et al., 2001, 2002; Palomba et al., 1997; Schupp et al., 2000). Keil et al. (2001, 2002) also demonstrated that both the P300 and the late positive slow wave show an arousal-related signal enhancement with largest differences in late VEPs as a function of emotional arousal for electrode sites near Pz (e.g. Cuthbert et al., 2000; Palomba et al., 1997). In an emotional picture viewing paradigm Keil et al. (2002) examined minimum norm estimation and showed maximum dipole strength over posterior sites, near posterior parietal and temporo-occipital cortex for the P300 and positive slow wave. These effects have been theoretically related to "motivated attention", suggesting that motivationally relevant stimuli naturally arouse and direct attentional resources so that emotional stimuli are processed preferentially (e.g. Keil et al., 2002; Lang et al., 1997). In general, the P300 component represents an index of processing capacity, attention, motivational relevance as well as task difficulty, and is influenced by biological processes such as the arousal state of subjects assessed by self-report measures or physiological performance (Polich and Kok, 1995). It appears as a distinct positive, relatively large wave, peaking from approximately 300 ms to 600 ms post stimulus (Kok, 1997; Polich and Kok, 1995; Spencer et al., 2001). The late positive slow wave to emotional pictures occurring as a sustained late positive wave and beginning at approximately 500 ms has been interpreted as reflecting sustained and high-level processing in which sustained attention is allocated to motivationally relevant and emotionally salient cues (Cuthbert et al., 2000; Keil et al., 2002).

The main hypothesis of the present study was that good heartbeat perceivers showed a more intense subjective emotional experience as well as a more intense processing of emotional pictures as is reflected in higher P300 and late positive slow wave amplitudes for emotional stimuli compared to poor heartbeat perceivers. We examined self-rated valence and arousal as well as P300 and slow wave amplitudes elicited by visual emotional stimuli.

This study aimed at replicating and extending results by Pollatos et al. (2005b) that demonstrated greater positive slow wave amplitudes as well as greater self-rated arousal for emotionally arousing pictures in good heartbeat perceivers. In the Pollatos et al. (2005b) study, the authors did not report emotion-specific results for the P300 latency range. As to the differences between good and poor heartbeat perceivers as well as regarding the correlations between heartbeat perception and P300 amplitudes, Pollatos et al. (2005b) reported significantly greater P300 amplitudes for affective and neutral pictures in good compared to poor heartbeat perceivers and only reported an emotionally non-specific positive correlation between heartbeat perception and mean P300 amplitude across emotion contents. Because of the fact that the P300 amplitude is sensitive to psychophysiological arousal (Polich & Kok, 1995) and has been shown to be enhanced by emotionally arousing pictures (e.g. Cuthbert et al., 2000; Keil et al., 2001, 2002; Palomba et al., 1997), as has been mentioned before, we expected emotion-specific differences between good and poor heartbeat perceivers in the P300 latency range as well as emotion-specific associations between heartbeat perception and P300 reactivity. P300 and positive slow wave reflect similar processes. Both components signal the greater allocation of perceptual processing resources to motivationally relevant input and reflect the elaborate and higher order processing of such input (e.g. Cuthbert et al., 2000; Keil et al., 2001, 2002; Kok, 1997; Schupp et al., 2004). Thus, both "late" components should be associated with heartbeat perception in an emotion-specific way. Bearing in mind that interoceptive sensitivity should be associated with a greater experiencing and processing of those stimuli that are emotionally arousing, but not of stimuli lacking in motivational relevance, our study tried to re-examine and to ameliorate the design of the study by Pollatos et al. (2005b) (see Materials and methods section). Furthermore, Pollatos et al. (2005b) reported a significant correlation between heartbeat perception and the mean arousal score of the subjective ratings (i.e. the mean arousal ratings of emotionally arousing as well as neutral picture categories). This finding per se does not allow a sufficient interpretation of the results regarding the association between interoceptive sensitivity (i.e. heartbeat perception) and the emotionally arousing aspect of emotional experience.

2. Materials and methods

2.1. Participants

Thirty-seven right-handed students (male: 19; female: 18) of the University of Munich with normal vision participated in the study. Their age ranged from 20–43 years. All subjects gave informed consent and obtained class credits.

2.2. Stimuli and design

While Pollatos et al. (2005b) only used 60 pictures (20 pleasant, 20 unpleasant, 20 neutral), in this study 120 colored pictures were selected from the International Affective Picture System (IAPS) (Center for the Study of Emotion and Attention, 1999), consisting of 40 highly arousing pleasant, 40 neutral, and 40 highly arousing unpleasant images. We chose a higher number of pictures in order to improve the signal to noise ratio for evoked potentials. The pictures were chosen according to the normative ratings of the IAPS (Lang et al., 1999). Pleasant pictures included erotic couples and scenes and happy families. Neutral pictures depicted household objects and neutral faces, and unpleasant pictures showed scenes of threat and attack. Normative ratings of valence for the pictures differed significantly (pleasant: 6.70, neutral: 4.94, unpleasant: 2.17; F (3, 843) = 47.59, $p < 0.001$) as did normative ratings for arousal (F (3, 844) = 101.07, $p < 0.001$). Neutral images were significantly less arousing (mean: 2.65, post-hoc LSD $p < 0.001$) than both pleasant (mean: 6.30) and unpleasant pictures (mean: 6.48) (e.g. Keil et al. 2002; Lang et al., 1999). Pleasant and unpleasant pictures did not differ with respect to normative arousal ratings (post-hoc LSD $p > 0.05$).

Compared to Pollatos et al. (2005b), who picked pictures that varied widely in content and affective tone regarding valence as well as arousal, we selected only highly arousing pictures of different valence according to the normative IAPS ratings. This was done to focus on differences between good and poor heartbeat perceivers in the arousal dimension of emotion. Thus, pleasant and unpleasant pictures differed maximally in their valence, but not in arousal, and there were maximally pronounced differences between the arousal of pleasant and neutral as well as unpleasant and neutral pictures, respectively.

The order of the pictures was arranged so that four blocks of 10 pleasant, four blocks of 10 unpleasant and four blocks of 10 neutral pictures were shown. The order of the blocks of pictures was pseudo-randomized with the restriction that each block followed a block of pictures of different valence. Emotional images were presented on a 19-in. computer screen with a frame refresh rate of 60 Hz. The screen was placed approximately 1.5 m in front of the viewer. The visual angle of the picture presentation was 15° horizontally and 11° vertically. Each picture was presented for 6000 ms, with intertrial intervals varying between 6000 and 12,000 ms. Possible luminance differences between pleasant, neutral and unpleasant pictures were controlled for using a Gossen Lunasix Exposimeter that allows measuring degrees of luminance.

2.3. Electrophysiological recordings

EEG activity was recorded continuously from 64 leads with a DC amplifier in AC mode (bandpass: 0.01–100 Hz; SYNAMPS, Neuroscan) and digitized at a rate of 500 Hz. Electrode positions were determined by an electrode cap (easy cap, Falk Minow Services) at equidistant positions (Fig. 1). Cz was used as a recording reference and the ground electrode was placed on the left cheek. Horizontal and vertical electrooculograms (EOG) were recorded by electrodes placed above and below the left eye (VEOG) and lateral to the outer canthus of each eye (HEOG). Impedances were kept below 5 kΩ. Offline, the EEG was re-referenced to linked mastoids.

2.4. Assessment of heartbeat perception

ECG was measured by means of lead I, Einthoven, using nonpolarizable Ag–AgCl electrodes. The signals were recorded (sampled at 1 kHz) and analyzed by a computer-based data acquisition system, MP150, version 3.7.2., and the corresponding software AcqKnowledge (BIOPAC Systems Inc., Santa Barbara, CA). The subjects were told to find a comfortable position and to sit as still as possible during data acquisition.

During the heartbeat detection task, subjects were asked to concentrate on their cardiac activity and to count their own heartbeats between onset and offset of a soft tone. They were told not to take their own pulse or try any other physical manipulations which could facilitate the detection of heartbeats. After the termination of the tone the participants had to report the counted number of heartbeats. The task was performed three times while the ECG was recorded, with time intervals lasting 25, 35 and 45 s, respectively. The three perception periods were separated by rest periods (30 s). The accuracy of heartbeat perception was quantified as a heartbeat perception score: Perception score = 1/3 Σ (1 − (|recorded heartbeats − counted heartbeats|) / recorded heartbeats). The maximum score of 1 indicates absolute accurate heartbeat perception.

Subjects were divided into good and poor heartbeat perceivers according to the heartbeat perception scores. Consistent with Pollatos et al. (2005b) and others, subjects scoring above 0.85 were assigned to the good heartbeat perception group ($N = 17$), while the rest ($N = 20$) formed the group of poor heartbeat perceivers ($N = 20$). The selected cut off score of 0.85 was used to be consistent with former studies (e.g. Montoya et al., 1993; Pollatos and Schandry, 2004; Pollatos et al., 2005a, b; Schandry, 1981; Schandry et al., 1986) which demonstrated that the 0.85 scores provided meaningful differences between subjects differing in interoceptive sensitivity.

The validity of heartbeat detection and counting tasks providing methods for registering interoceptive sensitivity has been criticized in some studies (e.g. Knapp-Kline and Kline, 2005; Ring and Brener, 1996; Windmann et al., 1999). Especially, it has been suggested that heartbeat tracking scores may be based on beliefs about, or estimates of, heart rates rather than accuracy of

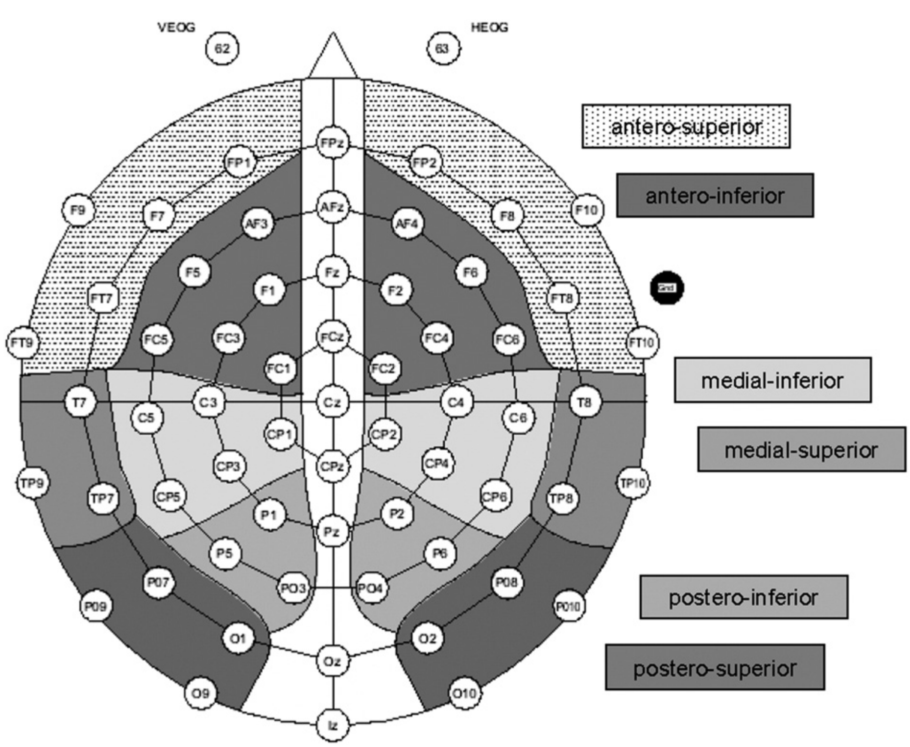


Fig. 1. Layout of the electrode array. Electrodes in the shaded clusters were grouped for statistical analysis. Frontal electrodes are shown at the top of the figure. Cz was used as a recording reference; data were arithmetically transformed to the linked ears reference offline.

heartbeat perception (e.g. Phillips and Jones, 1997; Ring and Brener, 1996; Windmann et al., 1999). As constant beliefs about heart rate should result in an obvious decline of heartbeat perception scores across the three consecutive time intervals of increasing duration (25, 35, 45 s) in our heartbeat counting task, we tried to examine these possible biases by looking for any conspicuous declines in the average heartbeat perception scores across the consecutive heartbeat perception intervals during the heartbeat counting procedure (Schandry, 1981). The latter could raise concerns of the validity of the heartbeat counting task.

2.5. Procedure

After arrival at the laboratory, subjects were informed about the experimental procedure and informed consent was obtained. Then, they filled in a form concerning personal data, such as age and educational level. Participants were then led into a sound-attenuated, dimly lit chamber, connected to the adjacent equipment room by intercom, and were fitted with Ag–AgCl adhesive disposable electrodes for ECG recording and completed the heartbeat perception procedure. Then, the scalp electrodes and the EOG electrodes were attached. In a training procedure, subjects were presented some pictures from each affective category in order to familiarize them with the presentation routine. These presented pictures were not part of the experimental set. During this procedure, participants were trained to maintain gaze on the center of the screen and to avoid explorative eye movements. Subjects were instructed to view the pictures while they were presented on the screen and rate the pictures for pleasantness and arousal after the viewing procedure.

Subsequently, subjects viewed the 120 selected experimental pictures chosen for differing arousal and valence. In contrast to Pollatos et al. (2005b) where subjects were asked to provide paper and pencil ratings of valence and arousal immediately after slide offset during the EEG picture viewing procedure, in this experiment, SAM ratings were accomplished after the EEG session was completed. Thus, after the picture presentation procedure participants viewed the pictures again and were asked to rate each picture for pleasure and arousal using a computer version of the Self-Assessment-Manikin (SAM; Lang, 1980) for exact registration of SAM ratings. The SAM allows the rating of pleasure (valence) and arousal on a 9-point scale, and consists of a graphic figure representing nine levels each of pleasure (valence) and arousal.

2.6. Data reduction and analysis

2.6.1. Heartbeat perception

Changes of means of heartbeat perception scores across each heartbeat counting time interval (25, 35 45 s) were analyzed using repeated-measures ANOVA with the factor "time interval" (3 levels: 25 s, 35 s, 45 s). Where appropriate, degrees of freedom were adjusted according to Greenhouse and Geisser (1959). Uncorrected F-values are reported together with the Greenhouse–Geisser corrected probability levels. For evaluation of significant ($p < 0.05$) main effects, critical differences were determined using the Scheffé procedure.

2.6.2. SAM ratings

Means of valence and arousal ratings were calculated for the three emotion contents, respectively. The SAM pleasure and arousal ratings were evaluated by means of repeated-measures analysis of variance (ANOVA) with factors of "Emotion Content (3 levels: pleasant, unpleasant, neutral) and "Heartbeat Perception Group" (2 levels: good heartbeat perceivers, poor heartbeat perceivers). Where appropriate, degrees of freedom were adjusted according to Greenhouse and Geisser (1959). Uncorrected F-values are reported together with the Greenhouse–Geisser corrected probability levels. For evaluation of significant ($p < 0.05$) main and interaction effects, critical differences were determined using the Scheffé procedure.

In order to take into account that heartbeat perception can be considered as a continuous dimension, non-parametric Spearman–Rho correlation coefficients (r_s) were calculated between the heartbeat perception score and both the mean SAM arousal and pleasure ratings for pleasant, unpleasant and neutral pictures. Furthermore, correlations between emotional difference scores (emotionally pleasant – neutral pictures; emotionally unpleasant – neutral pictures) for the SAM ratings and heartbeat perception score were examined, and partial correlations were calculated between the heartbeat perception score and SAM arousal ratings, controlling for pleasure ratings.

2.6.3. EEG analysis

The EEG record was examined for EOG, muscle activity, and other sources of artifacts. EOG correction for blinks was performed by the analysis software (Brain Vision) based on the blink correction method described by Gratton et al. (1983). EEG epochs were rejected from the analysis if the voltage exceeded ± 80 μV in any channel. Prior to averaging, trials contaminated by artifacts were eliminated (approximately 7% of the trials). The EEG was filtered with a bandpass of 0.01–40 Hz, and averaged offline. EEG sweeps were triggered by the onset of picture presentation. Epochs of 1100 ms (100 ms pre-, 1000 ms post-onset) were obtained for each stimulus from the continuously recorded EEG. The mean voltage of a 100 ms segment preceding picture onset was subtracted as the baseline.

For the purpose of statistical analysis, the mean voltages of the averaged visually evoked potentials (VEPs) were obtained for 12 scalp areas, formed by crossing hemisphere (left/right) with horizontal plane (anterior, medial, posterior), and vertical plane (inferior, superior), based on recording sites of the international 10–20 system (Keil et al., 2002). The locations of these regions with respect to sites of the international 10–20 system are shown in Fig. 1. Mean voltages in these regions were assessed in the P300 (290–500 ms) (Keil et al., 2001; Palomba et al., 1997; Pollatos et al., 2005b) as well as in the slow wave window (550–900 ms) (Cuthbert et al., 2000; Keil et al., 2002; Pollatos et al., 2005b). The data were submitted to repeated-measures analysis of variance (ANOVA) with factors of "Emotion Content" (pleasant, unpleasant, neutral), "Laterality" (left hemisphere, right hemisphere), "Region" (antero-inferior, antero-superior, medial-inferior, medial-superior, postero-inferior, postero-superior) and "Heartbeat Perception Group" (good heartbeat perceivers, poor heartbeat perceivers). Again, where appropriate, degrees of freedom were adjusted using the Greenhouse–Geisser method (Greenhouse and Geisser, 1959). Uncorrected F-values are reported together with the corrected p-values. For evaluation of significant ($p < 0.05$) main and interaction effects, critical differences were determined using the Scheffé procedure.

Additionally, Pearson correlations were calculated between the heartbeat perception score and the mean amplitudes for pleasant, unpleasant and neutral pictures in both the P300 and slow wave window.

3. Results

3.1. Heartbeat perception

The mean heartbeat perception score was 0.75 (SD = 0.18). A total of 17 subjects (8 females) demonstrated a heartbeat perception score above 0.85 and were assigned to the group of good heartbeat perceivers ($M = 0.90$; SD = 0.05). 20 subjects (10 women) with a heartbeat perception score below 0.85 formed the poor heartbeat perceivers group ($M = 0.64$; SD = 0.15). Women had a mean heartbeat perception score of 0.77 (SD = 0.14), and men had a score of 0.75 (SD = 0.21). There were no gender differences in heartbeat perception (one-way ANOVA: $F(1, 35) = 0.29$, $p > 0.05$).

The mean heartbeat perception scores did not significantly differ across the three consecutive heartbeat counting intervals ($F(2, 72) = 1.47$, $p > 0.05$, partial eta$^2 = 0.04$); 25 s: $M = 0.759$, SD = 0.17; 35 s: $M = 0.762$, SD = 0.17; 45 s: $M = 0.746$, SD = 0.19).

3.2. Gender and age

The groups of good and poor heartbeat perceivers did not differ in the distribution of gender (Chi$^2 = 0.86$, df = 1, $p > 0.05$) (see Table 1) nor in age (good heartbeat perceivers: $M = 25.2$, SD = 4.6, poor heartbeat perceivers: $M = 27.2$, SD = 6.5, $F(1, 35) = 1.17$, $p > 0.05$).

3.3. SAM rating

As expected, SAM pleasure ratings differed as a function of picture content (main effect of "Emotion Content": $F(2, 70) = 584.35$, $p < 0.001$, partial eta$^2 = 0.94$) with pictures (pleasant: $M = 6.98$, SD = 0.11, neutral: $M = 4.91$, SD = 0.03, unpleasant pictures: $M = 2.28$, SD = 0.10) all rated as significantly different from each other ($p < 0.001$). As far as the pleasure ratings are concerned, there was neither a significant main effect of "Heartbeat Perception Group" ($F(1, 35) = 1.80$, $p > 0.05$, partial eta$^2 = 0.05$) nor a significant "Emotion Content × Heartbeat Perception Group" interaction ($F(2, 70) = 0.99$, $p > 0.05$, partial eta$^2 = 0.03$). Good and poor heartbeat perceivers did not differ in their mean pleasure ratings for pleasant ($M = 6.97$, SD = 0.41 vs. 6.88, SD = 0.86), unpleasant ($M = 2.13$, SD = 0.47 vs. 2.42, SD = 0.61) and neutral ($M = 4.86$, SD = 0.15 vs. 4.95, SD = 0.24) pictures (see Fig. 2).

Table 1
Distribution of gender in the groups of good and poor heartbeat perceivers

	Men	Women	Total
Good heartbeat perceivers	9	8	17
Poor heartbeat perceivers	10	10	20
Total	19	18	37

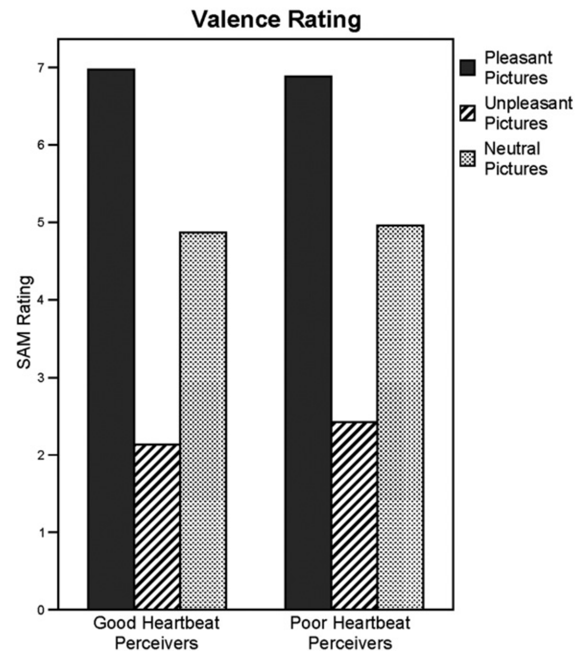
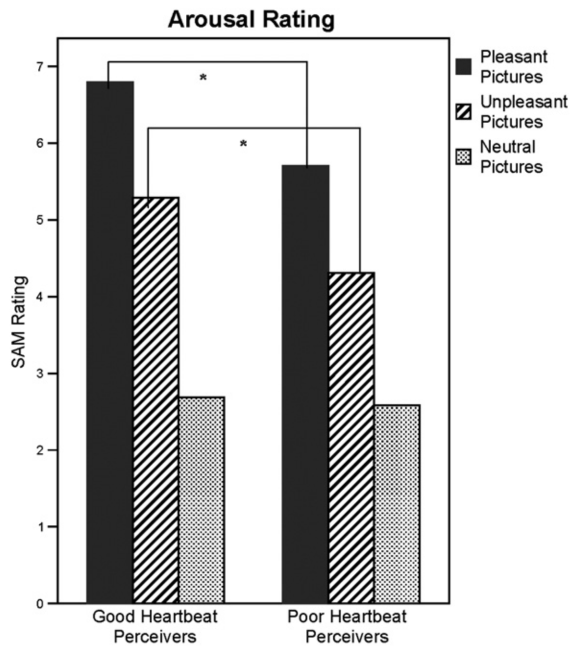


Fig. 2. SAM-valence-ratings of good and poor heartbeat perceivers for pleasant, unpleasant and neutral pictures.

Arousal ratings also differentiated picture categories (main effect of "Emotion Content": $F(2, 70) = 171.86$, $p < 0.001$, partial eta$^2 = 0.83$), with higher arousal ratings for both pleasant pictures ($M = 6.26$, SD = 0.14, $p < 0.01$) as well as for unpleasant pictures ($M = 4.90$, SD = 0.22, $p < 0.01$) than for neutral pictures ($M = 2.64$, SD = 0.17). Pleasant pictures were also rated as significantly more arousing than unpleasant pictures ($p < 0.01$). The arousal ratings demonstrated a significant main effect of "Heartbeat Perception Group" ($F(1, 35) = 6.41$, $p < 0.05$, partial eta$^2 = 0.16$), with good heartbeat perceivers ($M = 4.92$, SD = 0.21) demonstrating slightly but significantly higher arousal ratings than poor heartbeat perceivers ($M = 4.14$, SD = 0.19). Furthermore, the analyses for the arousal ratings revealed a significant "Emotion Content" × "Heartbeat Perception Group" interaction effect ($F(2, 70) = 3.82$, $p < 0.05$, partial eta$^2 = 0.10$). Scheffé testing showed that good heartbeat perceivers rated both pleasant ($M = 6.79$, SD = 0.59, $p < 0.05$) and unpleasant pictures ($M = 5.29$, SD = 0.43, $p < 0.05$) as being significantly more arousing than poor heartbeat perceivers (pleasant pictures: $M = 5.70$, SD = 1.05, unpleasant pictures: $M = 4.31$, SD = 1.75). The groups did not differ with respect to the neutral pictures (good heartbeat perceivers: $M = 2.68$, SD = 0.97 vs. poor heartbeat perceivers: $M = 2.60$, SD = 1.13, $p > 0.05$) (see Fig. 3).

Calculation of Spearman–Rho correlation coefficients demonstrated significant positive relationships between the heartbeat perception score and the mean arousal ratings of the unpleasant ($r_s = 0.32$, $p < 0.05$) and the pleasant pictures ($r_s = 0.55$, $p < 0.001$). There was neither a significant association between the heartbeat



Note: * indicates significant group differences (p < 0.05)

Fig. 3. SAM-arousal-ratings of good and poor heartbeat perceivers for pleasant, unpleasant and neutral pictures.

perception score and the arousal ratings of the neutral pictures (r_s = 0.18, $p > 0.05$) nor the pleasure ratings of the pictures (pleasant pictures: $r_s = 0.10$, $p > 0.05$, unpleasant pictures: $r_s = 0.09$, $p > 0.05$, neutral pictures: $r_s = -0.14$, $p > 0.05$). Examining the correlations between the difference scores of arousal ratings for emotional pictures and neutral pictures and the heartbeat perception score still demonstrated significant correlations (pleasant–neutral: $r_s = 0.36$, $p < 0.05$; unpleasant–neutral: $r_s = 0.30$, $p < 0.05$). Also, the calculation of partial correlations between emotional arousal ratings for pleasant, unpleasant and neutral pictures and the heartbeat perception score controlling for the respective pleasure ratings (e.g. Wiens et al., 2000) yielded significant results for emotionally arousing pictures (pleasant pictures: $r = 0.50$, $p < 0.01$, unpleasant pictures: $r = 0.32$, $p < 0.05$, neutral pictures: $r = 0.18$, $p > 0.05$). Thus, arousal ratings explained a significant proportion (pleasant pictures: 25% [$r^2 = 0.25$]), unpleasant pictures: 10% [$r^2 = 0.10$]) of variance, indicating that the association between heartbeat perception and arousal ratings remained significant after controlling for valence.

3.4. ERP morphology, topography and scalp voltages

As can be seen in Fig. 4, the visual inspection of the ERPs demonstrated five components: A N100, a P200, a N200, a P300 component and a late positive slow wave. Here, we focused on the P300 and the slow wave time window indicating the sustained and high-level processing of salient visual stimuli (e.g. Cuthbert et al., 2000; Keil et al., 2002). Fig. 5 shows the VEPs of good and poor heartbeat perceivers for pleasant, neutral and unpleasant pictures at the left antero-inferior region. Good and poor heartbeat perceivers showed explicit differences in the P300 (290–500 ms)

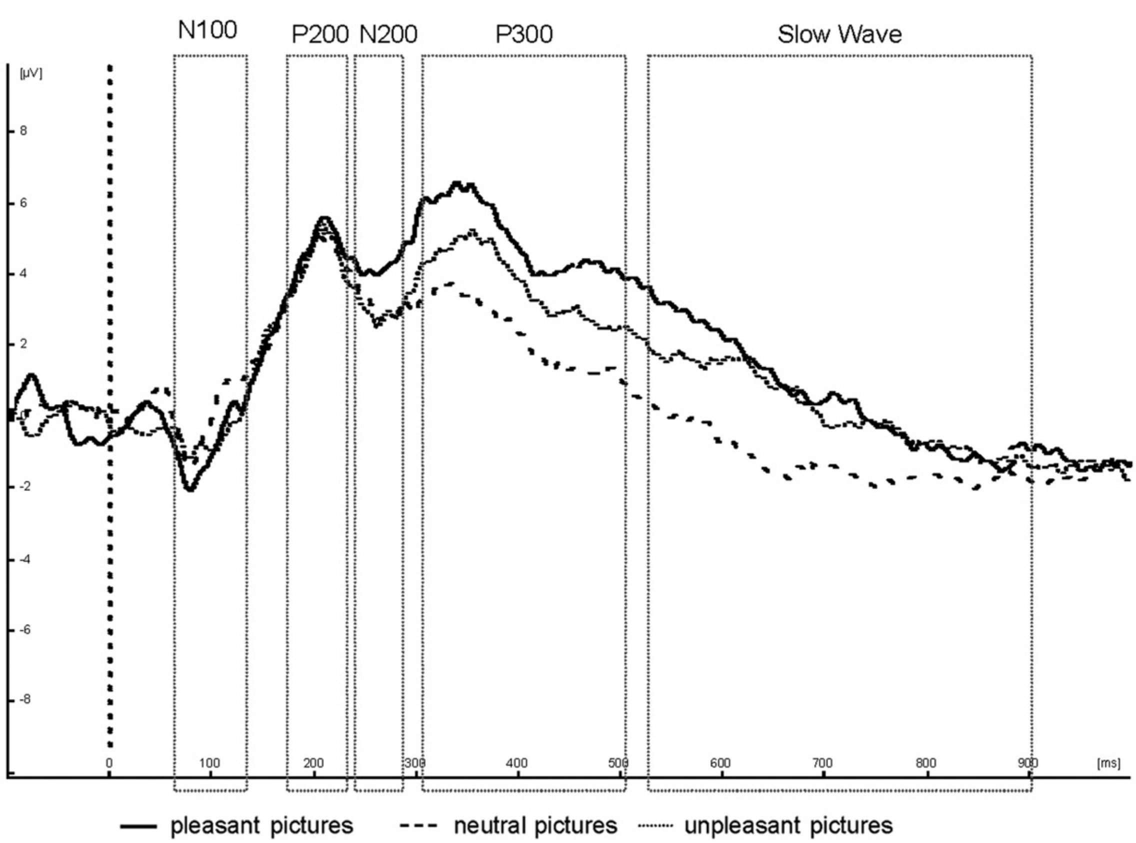


Fig. 4. Grand means (N=37) of the VEPs at the electrode Pz for pleasant, neutral and unpleasant images.

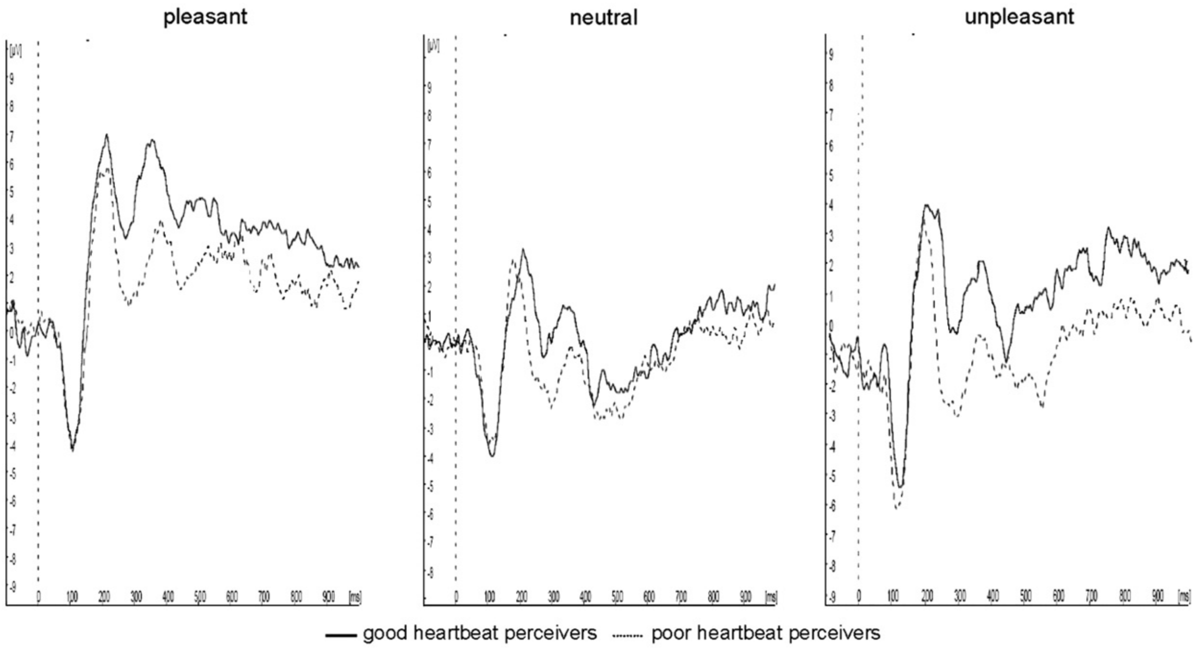


Fig. 5. VEPs of good ($N=17$) and poor ($N=20$) heartbeat perceivers at left antero-inferior electrode site (FC1) for pleasant, neutral and unpleasant stimuli.

and slow wave latency range (550–900 ms). Figs. 6 and 7 demonstrate brain maps of the VEPs in the P300 and slow wave window obtained for pleasant, neutral and unpleasant pictures, contrasting good and poor heartbeat perceivers.

3.5. P300 results

Statistical analyses for the P300 window (290–500 ms) showed that positivity of the P300 was greatest over posterior, both inferior ($M=3.71$ µV, SD=3.11 µV) and superior ($M=1.75$ µV, SD=2.04 µV), as well as medial-inferior ($M=2.00$ µV, SD=2.20 µV) sites (main effect of "Region": F (5, 175)=25.25, $p<0.001$, partial eta$^2=0.42$). This demonstrates that these regions contributed most to the positive potential in the P300 window ($p<0.05$). There was also a pronounced main effect of "Emotion Content" (F (2, 70)=42.81, $p<0.001$, partial eta$^2=0.55$). Scheffé-adjusted post-hoc testing demonstrated significantly greater voltages evoked by pleasant ($M=2.20$ µV, SD=3.11 µV, $p<0.01$) and unpleasant images ($M=1.37$ µV, SD=2.51 µV, $p<0.01$) compared to neutral pictures ($M=0.36$ µV, SD=2.82 µV). Pleasant pictures evoked greater P300 voltages than negative images ($p<0.01$) (Fig. 4).

Post-hoc testing of the significant "Region × Emotion Content" interaction effect (F (10, 350)=7.02, $p<0.001$, partial eta$^2=0.17$) demonstrated that antero-inferior, medial-inferior and postero-inferior sites showed a voltage amplitude enhancement of the P300 for pleasant and unpleasant compared to neutral content ($p<0.05$). In these regions there were also greater voltages in the P300 time window evoked by pleasant compared to unpleasant images ($p<0.05$).

Results demonstrated a significant "Emotion Content × Heartbeat Perception Group" interaction effect (F (2, 70)=4.47, $p<0.05$, partial eta$^2=0.13$). Post-hoc tests showed that good heartbeat perceivers had greater P300 voltages evoked by pleasant ($M=3.33$ µV, SD=1.43 µV, $p<0.05$) and unpleasant pictures ($M=2.15$ µV, SD=1.35 µV, $p<0.05$) compared to poor heartbeat perceivers (pleasant images: $M=1.22$ µV, SD=1.53 µV, unpleasant images: $M=0.65$ µV, SD=1.86 µV). Both groups did not differ in P300 amplitudes to neutral images (good heartbeat perceivers: $M=0.75$ µV, SD=1.19 µV, poor heartbeat perceivers: $M=-0.70$ µV, SD=1.74 µV; $p>0.05$) (see also Figs. 5 and 6).

A significant interaction effect between "Region" and "Heartbeat Perception Group" was observed (F (5, 175)=3.93, $p<0.01$, partial eta$^2=0.10$). Good heartbeat perceivers showed a more pronounced P300 over postero-inferior and postero-superior regions, as well as over medial-inferior and medial-superior sites ($p<0.05$).

Pearson correlations were calculated between the heartbeat perception score and the mean P300 amplitudes for pleasant, unpleasant and neutral pictures at medial and posterior sites, sites that have been shown to differentiate the groups in the ANOVA analyses. The results demonstrated significantly positive correlations between the heartbeat perception score and the P300 amplitudes for emotionally arousing pictures at medial-inferior (pleasant: $r=0.35$, $p<0.05$, unpleasant: $r=0.27$, $p<0.05$, neutral: $r=0.20$, $p>0.05$), medial-superior (pleasant: $r=0.34$, $p<0.05$, unpleasant: $r=0.31$, $p<0.05$, neutral: $r=0.21$, $p>0.05$), postero-inferior (pleasant: $r=0.40$, $p<0.01$, unpleasant: $r=0.37$, $p<0.05$, neutral: $r=0.22$, $p>0.05$) and postero-superior electrode sites (pleasant: $r=0.38$, $p<0.01$, unpleasant: $r=0.34$, $p<0.05$, neutral: $r=0.19$, $p>0.05$).

3.5.1. Slow wave results

The statistical analyses for the slow wave window (550–900 ms) demonstrated a significant main effect of "Region" (F (5, 175)=29.58, $p<0.001$, partial eta$^2=0.43$): Antero-inferior ($M=-0.02$ µV, SD=2.87 µV), medial-inferior ($M=1.97$, SD=2.26 µV) and postero-inferior ($M=4.08$, SD=3.01) sites

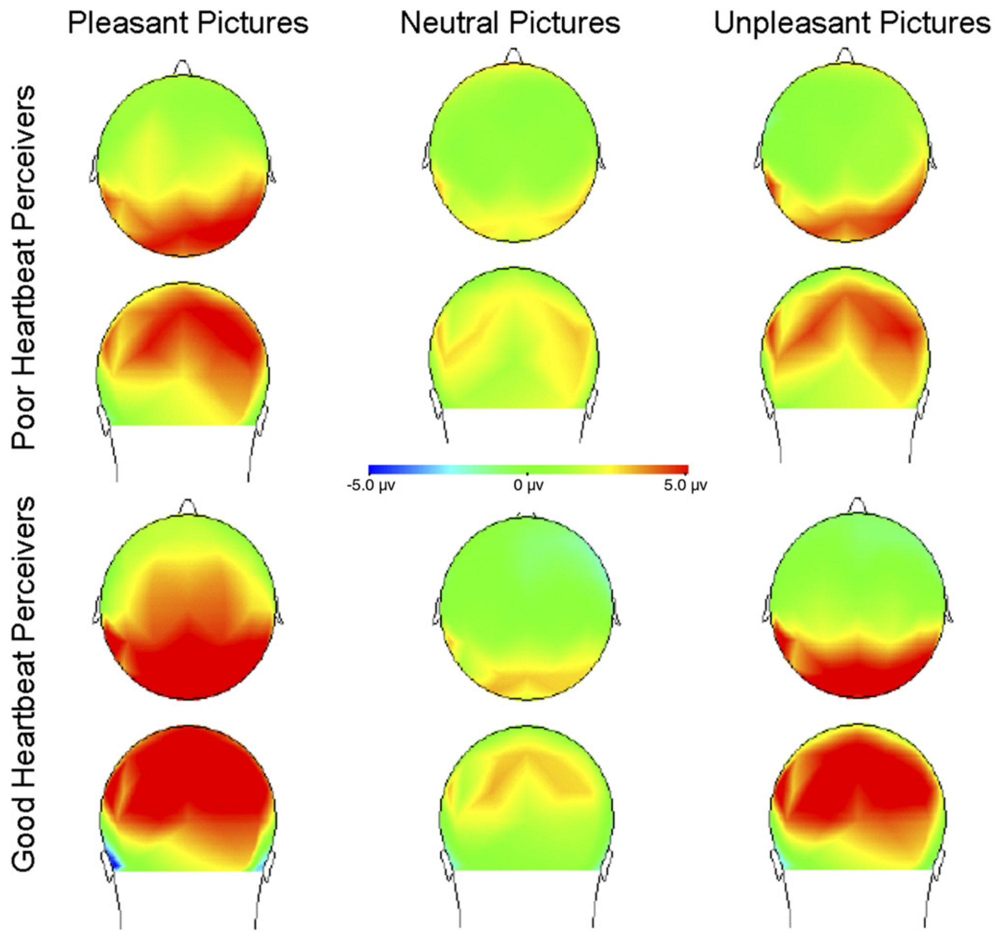


Fig. 6. Grand mean topography of the voltage distribution for the P300 latency range for poor and good heartbeat perceivers.

contributed most to the positive slow wave amplitude ($p<0.05$). A significant main effect of "Emotion Content" (F (2, 70)=31.39, $p<0.001$, partial eta^2=0.45) demonstrated that positivity for slow wave amplitudes was significantly greater for pleasant (M=2.21 µV, SD=2.03 µV, $p<0.001$) and unpleasant pictures (M=1.10 µV, SD=2.05 µV, $p<0.01$) than for neutral ones (M=0.45 µV, SD=2.08 µV). Also, pleasant pictures evoked significantly greater slow wave amplitudes than unpleasant pictures ($p<0.01$).

Post-hoc testing of the significant "Region × Emotion Content" interaction effect (F (10, 359)=8.60, $p<0.001$, partial eta^2=0.20) demonstrated that emotional pictures compared to neutral pictures evoked greater amplitudes at antero-inferior, medial-inferior, medial-superior and postero-inferior regions ($p<0.05$). Pleasant pictures evoked significantly greater amplitudes than unpleasant pictures at these electrode sites ($p<0.05$).

There was a significant main effect of "Heartbeat Perception Group" (F (1, 35)=10.19, $p<0.01$, partial eta^2=0.23). Good heartbeat perceivers (M=1.90 µV, SD=2.56 µV) demonstrated significantly greater slow wave positivity than poor heartbeat perceivers (M=0.47 µV, SD=1.78 µV).

Also, a significant "Emotion Content × Heartbeat Perception Group" interaction effect (F (2, 70)=4.55, $p<0.01$, partial eta^2=0.10) was observed. Post-hoc testing demonstrated that good heartbeat perceivers showed greater positive slow wave amplitudes evoked by pleasant (M=3.36 µV, SD=2.08 µV, $p<0.05$) and unpleasant pictures (M=1.63 µV, SD=2.82 µV, $p<0.05$) compared to poor heartbeat perceivers (pleasant images: M=1.12 µV, SD=2.16 µV; unpleasant images: M=0.35 µV, SD=2.12 µV). Both groups did not differ in slow wave amplitudes to neutral images (good heartbeat perceivers: M=0.36 µV, SD=2.05 µV, poor heartbeat perceivers: M=−0.80 µV, SD=2.07 µV, $p>0.05$) (see Figs. 5 and 7).

A significant interaction effect between "Region" and "Heartbeat Perception Group" (F (5, 175)=5.42, $p<0.01$, partial eta^2=0.13) demonstrated that good heartbeat perceivers showed significantly greater positive slow wave amplitudes especially at antero-inferior, medial-inferior and posterior sites than poor heartbeat perceivers ($p<0.05$).

Pearson correlations were calculated between the heartbeat perception score and the mean slow wave amplitudes for pleasant, unpleasant and neutral pictures at anterior, medial and posterior sites. The results demonstrated significantly positive correlations between the heartbeat perception score and the slow wave amplitudes for emotionally arousing pictures at antero-inferior (pleasant pictures: r=0.25, $p<0.05$, unpleasant pictures: r=0.24, $p<0.05$, neutral pictures: r=0.07, $p>0.05$), medial-inferior (pleasant pictures: r=0.34, $p<0.05$, unpleasant pictures: r=0.27, $p<0.05$, neutral pictures: r=0.11, $p>0.05$), postero-inferior (pleasant pictures: r=0.38, $p<0.01$, unpleasant pictures: r=0.32,

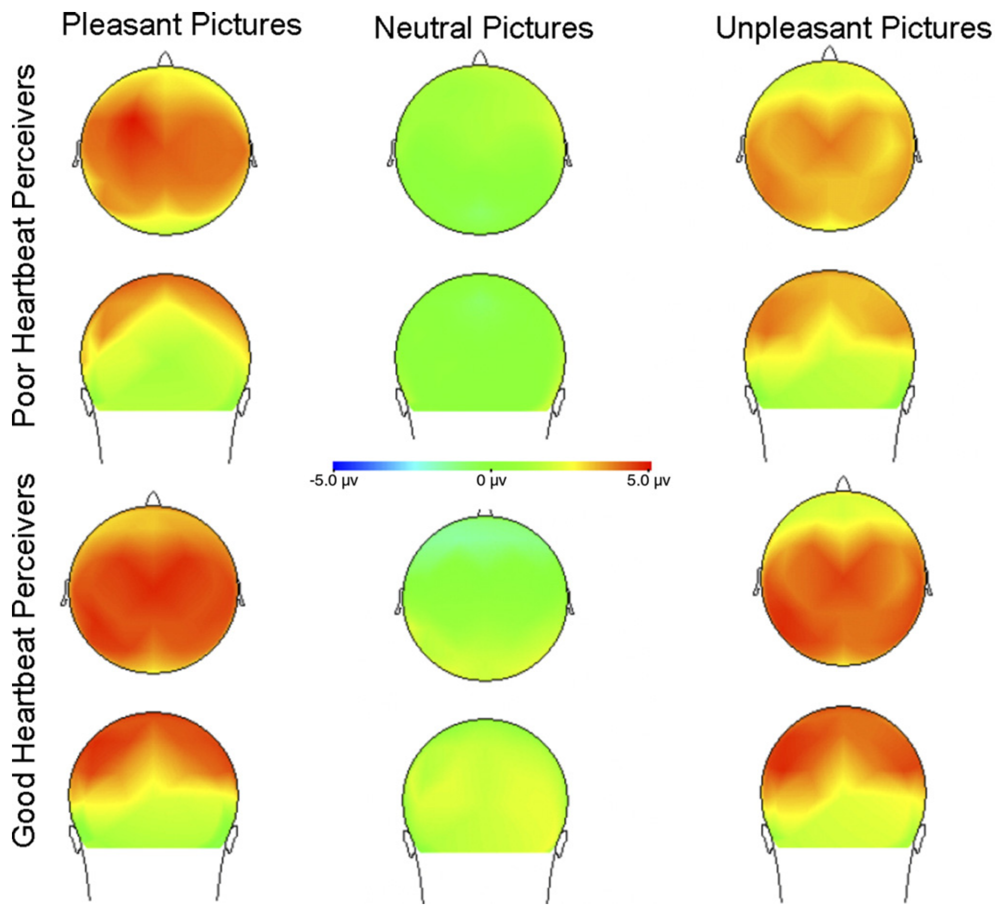


Fig. 7. Grand mean topography of the voltage distribution for the positive slow wave latency range for good and poor heartbeat perceivers.

$p<0.05$, neutral pictures: $r=0.25$, $p>0.05$) and postero-superior electrode sites (pleasant pictures: $r=0.37$, $p<0.05$, unpleasant pictures: $r=0.30$, $p<0.05$, neutral pictures: $r=0.11$, $p>0.05$).

4. Discussion

This study examined the question whether interoceptive sensitive persons experience and process emotional stimuli more intensely than persons with poor interoception. In accordance with our hypothesis, the ability to perceive one's heartbeat was significantly related to both emotional experience and emotional processing in the P300 and positive slow wave latency range.

We could replicate findings, showing that individuals who are highly sensitive to their visceral activity reacted with more intense affective responses to emotion-laden stimuli than individuals who are less sensitive (Critchley et al., 2004; Ferguson and Katkin, 1996; Hantas et al., 1982; Jones, 1994; Pollatos et al., 2005b; Schandry, 1981; Wiens et al., 2000; Wiens and Palmer, 2001). Additionally, good heartbeat perceivers demonstrated a greater arousing emotional experience only while viewing emotionally arousing pictures compared to poor heartbeat perceivers. The data demonstrated that there is a strong positive relationship between visceral sensitivity and the degree of the arousing experience of emotionally significant stimuli. The latter is supported by significant partial correlations between heartbeat perception score and arousal ratings of pleasant and unpleasant pictures while controlling for valence ratings.

This finding is corroborated by a study by Wiens et al. (2000), showing that good heartbeat perceivers rated emotional films more arousing than poor heartbeat perceivers. Wiens et al. (2000) also found significantly positive correlations between heartbeat detection ability and arousal ratings of emotional films while controlling for sympathetic arousal, gender and pleasantness ratings. The fact that interoceptive sensitivity is strongly related to the arousal dimension of emotional experience has also been demonstrated by Barret et al. (2004). The authors showed that people who were more sensitive to their heartbeats emphasized feelings of activation and deactivation when reporting their experiences of emotion ("arousal focus") over time more than those who were less sensitive.

Furthermore, results also demonstrated significant positive relations between heartbeat perception sensitivity and the intensity of experiencing both pleasant and unpleasant pictures when using emotional difference scores (pleasant – neutral; unpleasant – neutral) for the arousal ratings. This underscores that interoceptive sensitivity is related to the arousal dimension or the intensity of emotion (see also Wiens et al., 2000). By demonstrating that there is a specific association between heartbeat perception and emotional arousal ratings, our results extend recent findings by Pollatos et al. (2005b), showing significantly positive correlations between heartbeat perception and the mean arousal ratings for emotional and neutral pictures. Concerning the valence or pleasure ratings we could confirm data by Wiens et al. (2000) and Pollatos et al. (2005b), demonstrating that there were no significant differences between good and poor heartbeat perceivers in experiencing the valence of pleasant and unpleasant stimuli. Additionally, our data indicated that there was no significant correlation between heartbeat perception accuracy and valence ratings for emotional pictures, supporting the finding that heartbeat perception is related to the arousal but not the valence aspect of experiencing emotional stimuli. This is consistent with Schachter and Singer's (1962) suggestion that visceral arousal must be perceived to control emotional experience, while the quality or valence of an emotional state is defined by cognitive labelling.

It is a well known fact that emotional pictures are rated as more arousing than neutral ones (e.g. Lang et al., 1999; Schupp et al., 2004). Although the pictures in this study were chosen according to the normative IAPS ratings, and normative arousal ratings of the pleasant and unpleasant pictures did not differ significantly, we could also observe that our participants rated the pleasant pictures as more arousing than unpleasant pictures. We ascribe this result to the fact that we avoided presenting bloody and mutilation scenes, which have been shown to be most arousing in the sector of unpleasant valence (e.g. Schupp et al., 2004). Nevertheless, both picture categories, pleasant and unpleasant pictures, were rated significantly more arousing than neutral pictures, and good heartbeat perceivers differed significantly from poor heartbeat perceivers in an emotion-specific way.

As found in previous studies, our data showed that emotionally arousing stimuli induced a greater positivity in the P300 and positive slow wave latency window than neutral stimuli (e.g. Cuthbert et al., 2000; Keil et al., 2002), indicating that emotional stimuli are processed more intensely. This phenomenon can be interpreted in the context of "motivated attention", suggesting that motivationally relevant stimuli automatically direct attentional resources, are processed more deeply and thus provoke an arousal-related enhancement of VEPs (e.g. Cuthbert et al., 2000; Keil et al., 2002; Lang et al., 1997).

Comparable to Cuthbert et al. (2000) and Palomba et al. (1997) pleasant pictures evoked the greatest P300 as well as slow wave amplitudes. We also observed greater P300 and greater slow wave amplitudes for pleasant pictures compared to unpleasant pictures. According to our results of the SAM rating, we ascribe this result to our decision not to show mutilation scenes. These pictures have been demonstrated to prompt the greatest arousing effects in ERPs (e.g. Schupp et al., 2004). The same is reported for pictures depicting erotic scenes (Schupp et al., 2004).

As found, for example, in the study by Keil et al. (2002), our data also showed that especially posterior and medial electrode sites contributed most to the positive potential in the P300 window (e.g. Keil et al., 2002; Kok, 1997) with higher P300 amplitudes for emotional pictures compared to neutral pictures over these sites. Concerning the positive slow wave activity, the most enhanced amplitudes for affectively arousing pictures were seen at antero-inferior, medial and postero-inferior electrode sites. These findings are in accordance with results demonstrating the largest differences in late VEPs as a function of emotional arousal for electrode sites near Pz (Cuthbert et al., 2000; Keil et al., 2002; Palomba et al., 1997). Furthermore, assessing estimated sources using a minimum norm estimation Keil et al. (2002) demonstrated maximum dipole strength over posterior sites, near posterior parietal and temporo-occipital cortex for the P300 and positive slow wave in an emotional picture viewing paradigm.

Consistent with our hypothesis, good heartbeat perceivers showed significantly greater P300 and slow wave amplitudes in response to emotionally arousing pictures than was true for poor heartbeat perceivers. Our results confirm and extend findings by Pollatos et al. (2005b): while Pollatos et al. (2005b) observed significant emotion-specific differences between good and poor heartbeat perceivers in the positive slow wave amplitudes but not in the P300 latency range, our results made clear that good heartbeat perceivers exhibited both significantly greater slow wave and P300 amplitudes specifically to emotionally arousing pictures. This is in accordance with findings showing that both P300 and positive slow wave are enhanced by emotionally arousing pictures (e.g. Cuthbert et al., 2000; Keil et al., 2001, 2002; Palomba et al., 1997) and reflect similar processes related to emotional arousal and the elaborate processing of emotionally significant input (e.g. Cuthbert et al., 2000; Keil et al., 2001, 2002; Kok, 1997; Polich and Kok, 1995; Schupp et al., 2004). Good compared to poor heartbeat perceivers demonstrated more pronounced P300 amplitude at medial and posterior electrode sites, as well as a more enhanced positive slow wave amplitude at antero-inferior, medial-inferior and posterior electrode sites for emotionally arousing pictures. As has been stated afore, these sites denote those electrode sites that have been shown to reflect largest positivity when viewing emotional pictures.

The observed differences between the groups are underscored by significant correlations between heartbeat perception score, P300 and slow wave amplitudes for emotionally arousing, but not neutral pictures, at medial, posterior and antero-inferior electrode sites ranging between 0.27 and 0.40. These findings go beyond results by Pollatos et al. (2005b) and corroborate the significant association between heartbeat perception and the arousal dimension of processing emotional stimuli.

The most prominent differences between good and poor heartbeat perceivers as well as the significant associations between heartbeat perception and emotion processing at antero-inferior, medial and posterior electrode sites also suggest that the groups might differ particularly in their activation patterns at frontal, parietal and temporo-occipital structures. These are brain sites harboring structures such as the medial prefrontal cortex, cingulate cortex, insular cortex and somatosensory cortices, for example. These structures are considerably engaged in visceroception (e.g. Cameron, 2001; Critchley et al., 2004; Damasio et al., 2000; Pollatos et al., 2004) as well as autonomic-nervous control, visceral homeostatis (e.g. Critchley et al., 2000, 2003) and emotional processing (e.g. Bechara et al., 1997; Buchel et al., 1998; Canli et al., 2001; Damasio et al., 2000). This argues for the fact that the observed relations between heartbeat perception, emotional processing and emotional experience as well as the differences between good and poor heartbeat perceivers in "late" emotionally evoked potentials are mediated by different activation of those brain structures, contributing to both visceral, interoceptive and emotional processing (e.g. Pollatos et al., 2005b).

Exceeding this explanation, the observed group differences in P300 and slow wave amplitudes at posterior sites, reflecting activity in temporo-occipital cortical regions (e.g. Keil et al., 2002) could also shed light on interesting associations between interoceptive sensitivity and the sensory visual processing of emotional arousing pictures. For example, Keil et al. (2002) demonstrated maxima in dipole strength for P300 and positive slow wave amplitudes to emotional pictures in posterior and in occipital-temporal regions, and strongest effects of emotional content in posterior sites, near occipital-temporal cortex and posterior parietal cortex. The authors (Keil et al., 2002) suggest at least slow wave activity to be a correlate of longer lasting, higher order processing in occipito-temporal structures. The facilitated processing of emotionally arousing visual stimuli in the visual, occipital cortex has been shown to be associated with re-entrant processing between amygdala and inferotemporal brain structures in the ventral visual stream (e.g. Anderson and Phelps, 2001; Bradley et al., 2003; Vuilleumier et al., 2004). Thus, also these mechanisms and connections might be positively associated with interoceptive sensitivity.

As heartbeat detection is reported to be correlated with the detection of signals of other autonomically innervated organs (Whitehead and Drescher, 1980), our data suggest that “interoceptive sensitivity” is not only strongly associated with the intensity of emotional experience but also the central nervous processing of emotionally arousing stimuli. The results demonstrated that the self-perception of bodily signals, definitely also occurring in an emotional setting, is associated with a higher level of emotional arousal. The latter is reflected in both emotion-related brain activity and reported intensity of emotions. Thus, the findings of this experiment are consistent with former findings (Barrett et al., 2004; Pollatos et al., 2005b; Schandry, 1981; Wiens et al., 2000) showing that heartbeat detection, as an index of self-perception of visceral activity, is associated with the intensity of emotional experience but not with valence. Additionally, the study showed that this arousal related difference between the groups is also reflected in the central processing of emotionally salient stimuli, supporting the hypothesis that the feedback of bodily states is mediated by the arousal aspect of activation (e.g. Critchley et al., 2002; Damasio, 1994; Lane et al., 1999).

The results of this study lend support to hypotheses inferable from theories and findings, suggesting a pronounced link between visceral awareness, feelings and emotion processing (e.g. Blair and Cipolotti, 2000; Damasio, 1994, 1999; Critchley et al., 2004; Cameron, 2001; James, 1894). Above all, the data call attention to individual differences in the extent of interoceptive sensitivity for emotion processing, suggesting that highly visceroceptive persons, because of a more precise perception and processing of visceral signals (Critchley et al., 2004; Pollatos and Schandry, 2004), process emotional stimuli more intensely and experience a higher affective arousal while processing emotion-laden material.

Going beyond the above mentioned aspects, the relationship between heartbeat perception, emotional experience and emotion processing could be integrated within a hypothetical model of potential causal links between interoception and emotional experience by Wiens (2005). This model distinguishes between different aspects of interoception: interoception is divided into the central representation of feedback from the whole body (e.g. anterior insula), the “perception of actual physiological changes”, and the “perception of illusory physiological changes”. Whereas “first-level emotional experience” (phenomenology) is affected only by the central representation of feedback from the body, “second-level emotional experience” (awareness) is also affected by the perception of actual and illusory physiological changes. According to this model, in the absence of first-level experience, second-level experience reflects both the perception of actual and illusory physiological changes. This perception then triggers an attribution process according to culture-specific emotion schemata. According to Wiens (2005), interoceptive sensitivity (heartbeat detection) affects this process by allowing better discrimination between actual and illusory physiological changes. Thus, our results could reflect the influence of interoceptive sensitivity on emotional experience and emotional processing.

However, these results cannot per se give evidence for a causal relationship between interoceptive sensitivity and the intensity of emotional experience and emotion processing, as there is the possibility that some yet unidentified and uncontrolled third factor influenced this association. For example, although heartbeat perception is commonly treated as an index of conscious awareness of interoceptive processes, it might be confounded by other variables, such as differences in physiological arousal, and thus might index something else than interoception (e.g. Wiens, 2005). Also, there are some findings suggesting that heartbeat perception is positively influenced by beta adrenergic influences on the myocardium and that good heartbeat detectors demonstrated greater inotropic cardiovascular reactivity to mental stress (e.g. Eichler and Katkin, 1994) and greater emotional facial expressiveness to emotion-eliciting slides (Ferguson and Katkin, 1996). Eichler and Katkin (1994) suggested that subjects who are good at heartbeat perception may be those who are more often autonomically aroused and have had greater experience with the perception of heartbeats as a result of their greater inotropic cardiovascular activity to psychological stress. If this was the case, our findings could reflect differences in peripheral and/or central psychophysiological reactivity, rather than pure effects of interoceptive sensitivity. Nevertheless, there are also findings showing a lower heart rate in good heartbeat perceivers at rest (e.g. Knapp-Kline and Kline, 2005) as well as a more pronounced inhibition of facial expressiveness in good heartbeat perceivers (Ludwick-Rosenthal and Neufeld, 1965). Additionally, there is evidence demonstrating no significant differences in physiological arousal between good and poor heartbeat perceivers, neither in emotionally arousing situations nor at rest (e.g. Ferguson and Katkin, 1996; Hantas et al., 1982; Schandry, 1981; Wiens et al., 2000). The latter suggests that good heartbeat perceivers experience and process emotional stimuli more intensely because of more adequate self-perception of their visceral activity and not because of greater physiological arousal.

Further studies are necessary, examining physiological measures associated with heartbeat perception and emotion processing in order to shed light on the question whether the relationship between visceral self-perception and the intensity of emotion processing is not confounded by visceral activity. However, although confounding effects in heartbeat perception cannot be ruled out completely, the results demonstrating anterior insula and anterior cingulate cortex activations in heartbeat perception (Critchley et al., 2004; Pollatos et al., 2005a) are consistent with processes involving interoception (Wiens, 2005).

Finally, it has been suggested that heartbeat detection and counting tasks, providing methods for registering interoceptive sensitivity may be based on beliefs about, or estimates of, heart rates rather than accuracy of heartbeat perception (e.g. Phillips and Jones, 1997; Ring and Brener, 1996; Windmann et al., 1999). However, there is also strong evidence based on fMRI and dipole source localization results (see also above), underscoring activation of the same specific brain structures (insula, cingulate cortices) during both the processes of heartbeat counting (where subjects concentrate on and count their own heartbeats) (Pollatos et al., 2004) and heartbeat detection tasks (in which subjects judge the timing of their own heartbeat relative to feedback tones) (Critchley et al., 2004), as well as during spontaneous heart activity (Pollatos et al., 2005a). These findings support the validity of heartbeat perception tasks in detecting processes involving interoception (see Wiens, 2005). Also, our data did not show any conspicuous declines in the average heartbeat perception scores across the three consecutive heartbeat perception intervals during the heartbeat counting procedure.

Appendix A

Pleasant pictures: 1050, 3015, 3053, 3100, 3102, 3110, 3120, 3140, 3180, 3301, 3350, 3500, 3530, 3550, 6212, 6230, 6250,6260, 6300, 6313, 6350, 6360, 6510, 6530, 6540, 6550, 6560, 6570, 9040, 9250, 9252, 9330, 9410, 9421, 9490, 9570, 9571, 9611, 9810, 9921.

Unpleasant pictures: 1310, 1650, 4220, 4235, 4310, 4460, 4490, 4520, 4599, 4607, 4608, 4611, 4650, 4651, 4652, 4658, 4659, 4660, 4664, 4666, 4669, 4670, 4680, 4681, 4687, 4689, 4690, 4770, 4800, 4810, 5621, 5623, 5626, 5629, 8030, 8034, 8080, 8180, 8370, 8400.

Neutral pictures: 2514, 5130, 5390, 5510, 5520, 5530, 5534, 7000, 7002, 7004, 7006, 7009, 7010, 7020, 7025, 7030, 7031, 7034, 7035, 7040, 7050, 7060, 7080, 7090, 7096, 7100, 7110, 7130, 7140, 7150, 7160, 7175, 7185, 7187, 7217, 7224, 7233, 7700, 7705, 7950.

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