Research Report

# On the relationship between interoceptive awareness, emotional experience, and brain processes

Olga Pollatos[a,*], Wladimir Kirsch[b], Rainer Schandry[a]

[a]Department of Psychology, Ludwig-Maximilans-University of Munich, Leopoldstr. 13, 80802 Munich, Germany
[b]Department of Psychology, Philipps-University of Marburg, Germany

## Abstract

The perception of visceral signals plays a crucial role in many theories of emotions. The present study was designed to investigate the relationship between interoceptive awareness and emotion-related brain activity. 44 participants (16 male, 28 female) first underwent a heartbeat perception task and then were categorised either as good ($n = 22$) or poor heartbeat perceivers ($n = 22$). A total of 60 different pictures (pleasant, unpleasant, neutral) from the International Affective Picture System served as emotional stimuli. EEG (61 electrodes) and EOG were recorded during slide presentation. After each slide, the subjects had to rate emotional valence and arousal on a 9-point self-report scale. Good heartbeat perceivers scored the emotional slides significantly more arousing than poor heartbeat perceivers; no differences were found in the emotional valence ratings. The visually evoked potentials of good and poor heartbeat perceivers showed significant differences in the P300 and in the slow-wave latency ranges. Statistical analyses revealed significantly higher P300 mean amplitudes for good heartbeat perceivers (averaged across all 60 slides) than for poor heartbeat perceivers. In the slow-wave range, this effect was found for affective slides only. Heartbeat perception scores correlated significantly and positively with both the mean arousal rating as well as with the mean amplitudes in the P300 time window and the slow-wave window. Our results demonstrate a strong relationship between the perception of cardiac signals and the cortical processing of emotional stimuli, as would be postulated for example by the James–Lange theory of emotions.
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## 1. Introduction

The perception of signals arising from the body plays an important role in many theories of emotions (so-called *peripheral theories of emotions*). Well-known examples are the theories by James [40], Schachter and Singer [70] and Damasio [29]. William James postulated that viscero-afferent feedback is closely linked to emotional experience, stating that "bodily changes follow directly the perception of the exciting fact, and that our feelings of the same changes as they occur IS the emotion" [40] The James theory is often referred to as the James–Lange theory due to the fact that Carl Lange, a Danish psychologist, proposed a similar theory in 1885 [56]. However, Lange's theory used substantially more physiological reasoning as opposed to psychological reasoning. The theory of James is still under investigation today and continues to be a topic of debate [4,30,53,66]. Schachter and Singer [70] agreed with James insofar as that visceral arousal is seen as a prerequisite for emotional experience. However, they emphasised the importance of cognitive attributions for the quality of the resulting emotional state. An example for a recent psychological theory incorporating the feedback from the periph-

* Corresponding author. Fax: +49 89 2180 5233.
*E-mail address:* pollatos@psy.uni-muenchen.de (O. Pollatos).

eral nervous system (somatosensory and visceral) is the somatic marker hypothesis by Damasio and colleagues [1,2,6,25,26,28,82]. The authors speak of the obligatory body-relatedness of feeling: "the body is the main stage for emotions, either directly or via its representations in somatosensory structures of the brain" (p. 287, [27]). Furthermore, it is pointed out [27] that the described mechanisms to engage in emotional behaviour are compatible with James' view, thereby adding a new dimension by stating that "the emotional responses target both the body proper and the brain".

## 1.1. Interoceptive awareness and emotional experience

James [40] stated that feelings originate from the perception of bodily states. Following this assumption, one may conclude that the extent of a person's sensitivity to bodily signals ("interoceptive awareness", "visceral perception") should be related to the experienced intensity of emotions. Individual differences in visceral perception have often been assessed by focussing on the cardiovascular system, and especially on the perception of heartbeats. Different heartbeat perception tasks have been developed and are widely used [11,12,57,64,71,74,83,85,89]. Substantial interindividual differences in heartbeat perception assessed under resting conditions have been shown in several studies [41,45,58,64,71,72,74,86,87,91]. Subjects with good heartbeat perception – from the described viewpoint of peripheral theories of emotions – should experience emotions more intensely due to their heightened ability to perceive their bodily states. Most of the studies addressing this question found a positive relationship between heartbeat perception and emotional experience [22,31,58,71,89]. Blascovich et al. [8], however, found a negative relationship between a questionnaire measure of affect intensity and heartbeat detection.

A direct consequence of the increased emotional experience of persons with good heartbeat perception pertains to emotion-related brain processes. It has to be assumed that brain structures, which are related to the processing of emotional stimuli, will reveal an enhanced activity in persons with good heartbeat perception as compared to those with poor heartbeat perception. These structures should be of relevance for both heartbeat perception and emotional experience and thus serve as an interface between the perception of bodily signals and the processing of emotional stimuli on the input side, and emotional experience on the output side.

Research performed with PET and fMRI has shown that cerebral processing of emotions involves structures that are also dealing with the regulation of bodily states: Damasio et al. [28] found that during the feeling of self-generated emotions, the somatosensory cortices, the insula, the anterior and posterior cingulated cortex, and nuclei in the brainstem are activated. Their findings are consistent with anatomic evidence that these regions are direct or indirect

recipients of signals from the internal milieu and viscera [60]. In the framework of Rolls [67], the orbitofrontal cortex, the somatosensory cortex and the amygdala are important structures for the processing of emotions. Some evidence exists for the right insula to play an important role in connecting emotional experience with interoceptive awareness [18,22,36,38,39,49,75]. In a recent fMRI study, Critchley et al. [22] could demonstrate that state anxiety was correlated with both interoceptive awareness as measured through a heartbeat perception task and the BOLD activity in the right insula. Taking these lines of research together, one might speculate that there are certain brain regions that both monitor the ongoing internal emotional state of the organism and are involved in the processing of emotions.

## 1.2. ERPs and emotion

Event related potentials (ERPs) of the EEG allow the investigation of the topographic distribution of cortical activity and the time course of the brain responses following the perception of emotional stimuli. Brain electrical responses to emotional stimuli have frequently been studied by using affective pictures as stimuli (e.g., [10,16,23,24,34,35, 48,59,77,84]). One major finding is a greater magnitude of the P300 amplitude in response to pictures with emotional content as compared to neutral pictures. The P300 component is assumed to be an index of attention, processing capacity, motivational relevance, and task difficulty. It appears as a relatively large, distinct positive wave, peaking from approximately 300 ms to 600 ms post stimulus, depending on the specific experimental manipulations [43,50,63,78]. Besides the P300, the so-called late-positive slow wave (a sustained late positive wave at 400 ms and beyond) shows sensitivity to emotional picture contents [24,29,48,59]. It is assumed that the positive slow wave reflects the continued perceptual processing of emotional information [24,50].

The enhanced brain electrical activity during viewing of pleasant and unpleasant pictures may indicate that emotional stimuli are processed preferentially [48,55]. This assumption is in accordance to many theorists who claim that the affect system has evolved from a motivational basis [35]. Biphasic theories of emotions describe emotions on the two dimensions pleasantness, respectively, valence and arousal [35,54,55]. While pleasantness stands for the quality of emotions, emotional arousal refers to the intensity of mobilization or energy [35]. In many studies, both dimensions were assessed by self-report measures and physiological variables like evoked potentials, heart rate or skin conductance (see [24]). Generally, affective pictures are rated as more arousing than neutral ones (e.g. [54]). Concerning the interaction between evoked potentials and arousal, Polich and Kok [63] pointed out that the P300 is influenced by biological processes like the arousal state of subjects assessed by physiological performance or self-report measures. In accordance to this assumption Cuthbert et al. [24] showed that late positive potentials (e.g., 700–

1000 ms post-stimulus) are specifically enhanced by pictures that are rated as more arousing. Also, Keil et al. [47] showed a modulation of late positive ERPs as a function of emotional arousal. Having in mind that former studies have shown an interaction between interoceptive awareness and the experienced intensity of emotions on the level of verbal report [22,31,58,71,89], one can assume that these observed differences in self-reported arousal correspond with analogous differences measured by evoked potentials. Especially the P300 component and the slow wave of the ERP, elicited by emotional stimuli, may be components sensitive for a modulation by interoceptive awareness.

The present study was designed primarily to investigate the cortical processes that are related to both interoceptive awareness and emotion-related brain activity. Thus, for good and poor heartbeat perceivers, visual evoked potentials elicited by emotional stimuli were analysed together with self-rated emotional experience.

In detail, the following hypotheses were examined:

(1) Subjects who perceive their heartbeats with high accuracy show higher arousal ratings to affective pictures.
(2) The heartbeat perception score and the subjective arousal rating are positively correlated.
(3) Good heartbeat perceivers display an enhancement in the P300 and slow wave components elicited by emotionally arousing pictures.
(4) The heartbeat perception score and the mean amplitude in the P300 time window as well as in the slow wave window are positively correlated.

## 2. Materials and methods

### 2.1. Subjects

The sample consisted of 44 students (16 male, 28 female) from the University of Munich. Subjects received €30 (about $30) for their participation. The mean age was 25.5 (SD 4.5) years ranging from 18 to 36 years of age. Subjects were recruited in such a manner that both groups (good/poor heartbeat perceivers) were composed of 22 participants with an equal number of males (8) and females (14). Specifically, we used a screening test and assessed heartbeat perception in about 140 subjects. According to their performance, 22 good heartbeat perceivers were identified. Subjects with poor heartbeat perception were then selected in order to be highly compatible concerning age and sex.

### 2.2. Stimulus material

The stimulus material consisted of 60 pictures chosen from the International Affective Picture System [17]. The selected pictures (see Appendix) varied widely in content

and affective tone regarding valence (from unpleasant to pleasant) as well as arousal (calm to arousing). According to the normative ratings of the IAPS (52), there were 20 pleasant (e.g., attractive nudes, romantic couples, cuddling animals, appetizing foods, and happy babies), 20 neutral (e.g., common household objects), and 20 unpleasant pictures (e.g., pictures of violent death, aimed guns, snakes, angry or starving people). Pleasant, neutral, and unpleasant slides differed significantly regarding valence (mean 7.4, 5.0 and 3.0, respectively; $F(2, 57) = 311.8$; $P < 0.001$) based on the normative valence ratings reported by Lang et al. [54]. Neutral pictures were significantly less arousing (mean 2.8; ANOVA: $F(2, 57) = 83.30$; $P < 0.001$; post hoc LSD tests: pleasant or unpleasant vs. neutral: 2.73 and 3.14, respectively; $P < 0.001$) than both pleasant and unpleasant slides (mean 5.5 or 5.9, respectively). Pleasant and unpleasant slides did not differ significantly regarding their normative arousal ratings (post hoc LSD tests: mean difference pleasant vs. unpleasant 0.41; $P > 0.05$).

Emotional slides were projected approximately at a distance of 1.9 m from the subjects' eyes. The visible size of the pictures was $75 \times 50$ cm, resulting in a picture presentation with a visual angle of 22° horizontally, and 15° vertically.

No luminance (measured with a Gossen Lunasix 3 Exposimeter) differences existed between pleasant, neutral and unpleasant slides (ANOVA, $F(2, 57) = 0.655$, $P = $ n.s.).

### 2.3. Procedure

On arrival, subjects were given written information about the experiment and informed consent was obtained. Next, they filled in a general form concerning personal data (e.g., age, educational level) and they were subsequently seated in a comfortable chair in a sound-attenuated chamber connected to the adjacent equipment room by intercom. After attachment of the electrode cap, the encephalic, the EOG and the ECG electrodes, the heartbeat perception tasks were performed. Eleven heartbeat-counting phases were employed. During all trials, participants were asked to count their own heartbeats silently. The beginning and end of the counting phases were signalled by a start and stop tone. After the stop signal, subjects were required to verbally report the number of counted heartbeats. Subjects were neither informed about the length of the counting phases nor about their performance. At the end of the heartbeat perception task, a pause of about 10 min took place.

In a training procedure, subjects were made familiar with the stimuli presentation routine and the rating of the pictures on two dimensions, namely affective valence and arousal on the basis of a paper and pencil version of the self-assessment manikin (SAM) [9].

The presentation of the emotional stimuli was as follows. A single experimental trial started with a fixation

slide (displaying a cross at the center of the screen) that was visible for 6 s. Then, an IAPS slide was presented for 6 s. Subjects were instructed to avoid exploratory eye-movements and eye-blinks and attentively view the pictures. Immediately after slide offset, the subjects were asked to provide valence and arousal ratings. These ratings were obtained using a paper and pencil form of the SAM. Pleasantness was rated on a 9-point scale ranging from very unpleasant/negative to very pleasant/positive. In the arousal rating, the 9-point-scale ranged from very low to very high. The rating interval lasted 15 s. Afterwards, the fixation slide was presented once again, followed by the next IAPS slide. The experiment continued in the sequence described above.

Overall, 60 trials divided into four blocks of 15 trials were presented. The order of the stimuli was pseudo-randomised under the restriction that the presentation of a series of three pictures belonging to the same subset should not occur. After each block, there was a break of 5 min. The entire experimental procedure lasted about 40 min.

### 2.4. EEG recording

EEG activity was recorded from 62 leads over both hemispheres with a DC amplifier (bandpass: 0.01–100 Hz; SYNAMPS, Neuroscan) and digitised at a sampling rate of 250 Hz. Electrode positions were determined through the electrode cap (easy cap, Falk Minow Services) at equidistant positions with 61 electrodes (see Fig. 1). The reference electrode was positioned at the tip of the nose and the ground electrode was placed on the left cheek. Offline, the EEG was re-referenced to linked mastoids.

Horizontal and vertical electrooculograms (EOG) were recorded with electrodes which were placed lateral to 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 kΩ.

### 2.5. ECG recording

The ECG was measured using nonpolarizable Ag–AgCl electrodes attached to the right mid-clavicle and
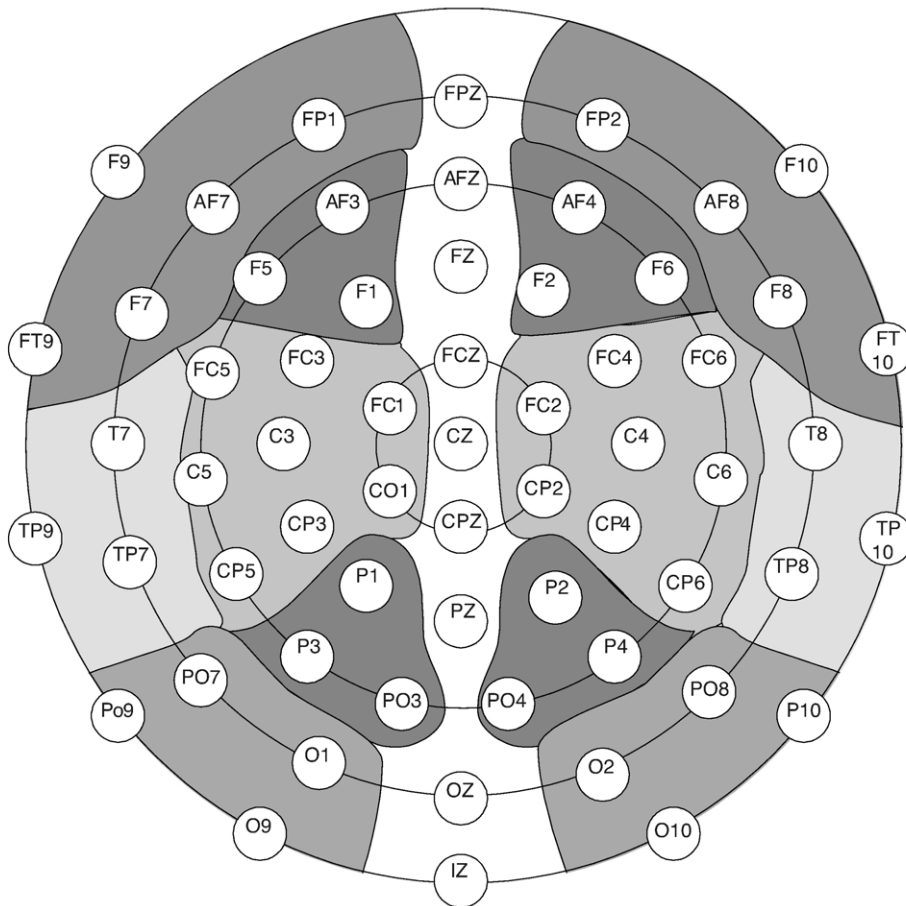


Fig. 1. Layout of the electrode array. Electrodes in the shaded clusters were grouped for statistical analysis. Frontal electrodes are shown at the top of the figure.

lower left rib cage. ECG activity was recorded analogous to the EEG with a DC amplifier (bandpass: 0.01–100 Hz; SYNAMPS, Neuroscan) and digitised at a sampling rate of 250 Hz. R-waves were detected online with a Schmitt-trigger and were stored on a separate trigger channel. Additionally, the raw ECG was stored in an analogous manner as the EEG.

### 2.6. Data Reduction and analysis

The EEG record was examined for EOG, muscle activity, and other sources of electrophysiological artefacts. The analysis software (Brain Vision) performed EOG correction for blinks based on the blink correction method described by Gratton et al. [33]. EEG epochs were rejected from the analysis if the scalp EEG exceeded ± 80 µV in any channel. Trials contaminated by artefacts were eliminated prior to averaging. This accounted for approximately 8% of the trials.

The EEG was filtered with a bandpass of 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.

For the purpose of statistical analysis, the mean voltages of the averaged visually evoked potential (VEPs) were obtained for 12 regions, formed by crossing hemisphere (right/left) with horizontal plane (anterior, medial, posterior), and vertical plane (inferior, superior). The locations of these regions with respect to sites of the international 10–20 system are shown in Fig. 1.

Mean voltages were assessed in three time windows, corresponding roughly to the N100 (100–150 ms), P300 (290–500 ms) and the slow wave window (550–900 ms). Main effects and interactions as well as between-group differences were investigated by submitting the data to ANOVAs with two levels of hemisphere (right/left), six levels of region (antero-inferior, antero-superior, medial-inferior, medial-superior, postero-inferior, postero-superior), three levels of emotion content (pleasant, unpleasant, neutral) and two levels of heartbeat perception (good/poor). Where appropriate, degrees of freedom were adjusted after Greenhouse and Geisser. In Results, uncorrected $F$ values are reported together with the Greenhouse–Geisser epsilon values and corrected probability levels.

### 2.7. Analysis of the SAM ratings

Mean valence and arousal ratings were calculated separately for the three emotion contents. Outlier analyses were performed on the subjects' mean valence or arousal scores. Subjects whose mean valence or arousal scores were more than two standard deviations above or below the mean scores were excluded from further analysis. Consequently, three subjects (two good heartbeat perceivers, one poor heartbeat perceiver) had to be excluded.

For the evaluation of significant main effects between group differences and interactions, the SAM valence and arousal ratings were submitted to repeated measure analyses (ANOVAs) with three levels of emotion content (pleasant, unpleasant, neutral) and two levels of heartbeat perception (good/poor). Where appropriate, degrees of freedom were adjusted according to Greenhouse and Geisser. Uncorrected $F$ values are reported together with the Greenhouse–Geisser epsilon values and corrected probability levels.

### 2.8. Correlation analyses

Non-parametric Spearman–Rho correlation coefficients were calculated between the heartbeat perception score on the one hand and the mean SAM arousal rating scores, as well as the mean amplitude in the P300 time window and the slow wave window on the other hand. In case of multiple testing regarding the P300 and the slow wave window, we corrected the probability level according to the Bonferroni procedure for all tests.

## 3. Results

### 3.1. Heartbeat perception

A heartbeat perception score was calculated as the mean score of eleven heartbeat perception intervals according to the following transformation:

FORMULA: $1/11\Sigma(1 - (\text{recorded heartbeats} - \text{counted heartbeats})/\text{recorded heartbeats})$

The mean heartbeat perception score was 0.78 (SD 0.19; minimum 0.19; maximum 0.98). Female subjects had a mean heartbeat perception score of 0.77 (SD 0.21; minimum 0.13; maximum 0.98), male subjects of 0.80 (SD 0.14; minimum 0.52; maximum 0.96). There was no significant difference between male and female subjects in relation to heartbeat perception (univariate ANOVA: $F(1, 42) = 0.24$; $P = $ n.s.).

A total of 22 subjects (14 female) with a score above 0.85 were assigned to the good heartbeat perceiver group. In this group, the mean heartbeat perception score was 0.92 (SD 0.04; minimum 0.87; maximum 0.98). The other 22 subjects (14 female) with a mean heartbeat perception score of 0.64 (SD 0.16; minimum 0.14; maximum 0.82) formed the group of poor heartbeat perceivers. The distribution of the heartbeat perception scores in both groups is summarized in Fig. 2. The selected cut off score of 0.85 was used in accordance to former studies [58,73] showing that this score is appropriate to distinguish between subjects who differ substantially in interoceptive awareness.
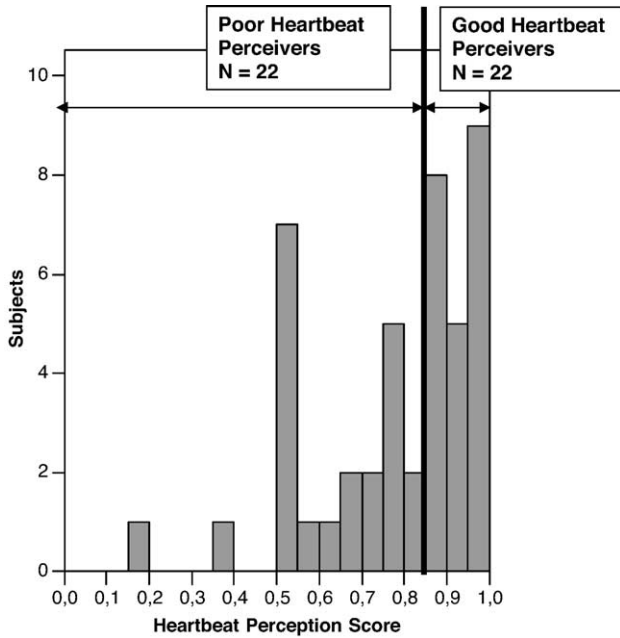
Fig. 2. Distribution of the heartbeat perception score ($N = 44$).

## 3.2. Morphology and topography of the visual evoked potentials

VEP traces at electrodes corresponding to 34 sites of the international 10–20 system are shown in Fig. 3. Visual inspection revealed five components (see the grand average in Fig. 4): An N100, a P200, an N200, a P300 and a slow wave. Fig. 5 displays the VEPs of good and poor heartbeat perceivers for pleasant, unpleasant and neutral pictures for the left anterior–superior region. In the latency ranges later than 250 ms, the potentials of good and poor heartbeat perceivers revealed significant differences. In accordance to former studies using emotional pictures (e.g. [48]), a time window of 100–150 ms was used to calculate the mean N100, a time window of 290–500 ms was used for the mean P300 and a time window of 550–900 ms was selected to calculate the mean slow wave voltage.

The brain maps in Figs. 6 and 7 illustrate the VEPs obtained for pleasant, unpleasant and neutral slides, contrasting good and poor heartbeat perceivers for the latency range of 290–500 ms and 550–900 ms.

## 3.3. Statistical analyses of the visual evoked potentials

### 3.3.1. N100 (100–150 ms)

A main effect for *Region* ($F(5, 210) = 55.24$, $P < 0.001$, $\eta^2 = 0.58$, $\varepsilon = 1.00$) was assessed; anterior and medial sites showed the strongest negativity as compared to posterior sites ($P < 0.05$).

A main effect for *Hemisphere* indicated a significantly higher mean activity in the right hemisphere ($F(1, 42) = 4.53$, $P < 0.05$, $\eta^2 = 0.10$, $\varepsilon = 0.55$).

Mean voltage in the N1 (100–150) time window resulted in a significant *Emotion Content × Region* interaction ($F(10, 420) = 20.59$, $P < 0.05$, $\eta^2 = 0.06$, $\varepsilon = 0.72$). Post hoc, Bonferroni-adjusted ANOVAs for each region indicated that effects of slide content were present at anterior–inferior, anterior–superior, and medial–superior sites. In particular, enhanced activity for pleasant as compared to unpleasant slides was assessed ($P < 0.05$).

### 3.3.2. P300 (290–500 ms)

A significant main effect of *Emotion Content* ($F(5, 210) = 14.90$, $P < 0.001$; $\eta^2 = 0.26$, $\varepsilon = 1.00$) was seen in the P300 time window. Post hoc, Bonferroni-adjusted ANOVAs indicated that the mean activity to pleasant slides (4.40 μV) was significantly higher than to unpleasant slides (3.63 μV; $P < 0.05$). Unpleasant slides evoked a significantly higher mean activity than neutral slides (2.68 μV; $P < 0.05$; compare Figs. 3 and 4). A main effect of Region ($F(5, 210) = 87.11$, $P < 0.001$; $\eta^2 = 0.68$, $\varepsilon = 1.00$) showed that medial and posterior sites contributed most to the positive potential in the P300 latency range.

A main effect of *Heartbeat Perception* ($F(1, 42) = 5.17$, $P < 0.05$; $\eta^2 = 0.11$, $\varepsilon = 0.60$) was observed. Good heartbeat perceivers (4.14 μV) revealed higher amplitudes than poor heartbeat perceivers (3.00 μV; see Figs. 4 and 6). In order to show the time course and the effect of heartbeat perception on both the P300 and the slow wave amplitude, Fig. 4 displays the left anterior–superior region.

Furthermore, a significant *Emotion Content × Region* interaction ($F(10, 420) = 4.33$, $P < 0.05$; $\eta^2 = 0.09$, $\varepsilon = 0.93$) was obtained. Anterior–superior, anterior–inferior and medial–inferior sites showed a voltage amplitude enhancement for pleasant pictures, compared to neutral and unpleasant content, whereas medial–superior and
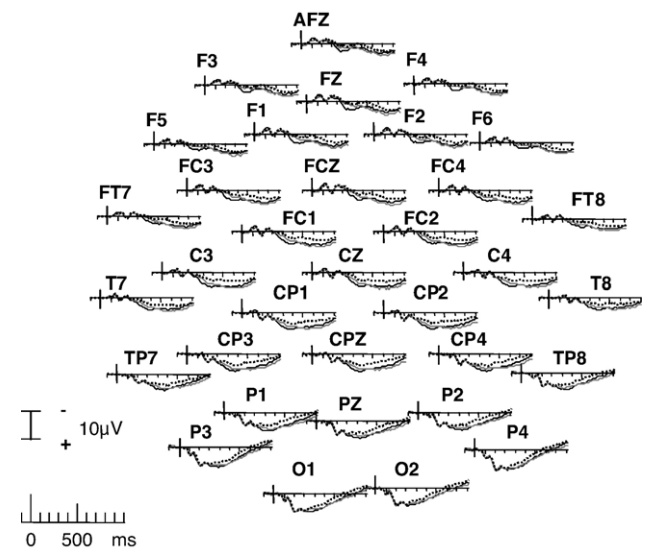


Fig. 3. Grand means ($N = 44$) event-related potentials at selected electrodes corresponding to the International 10–20 System, for pleasant (black), neutral (dashed), and unpleasant (gray) content. Note: positive is down.
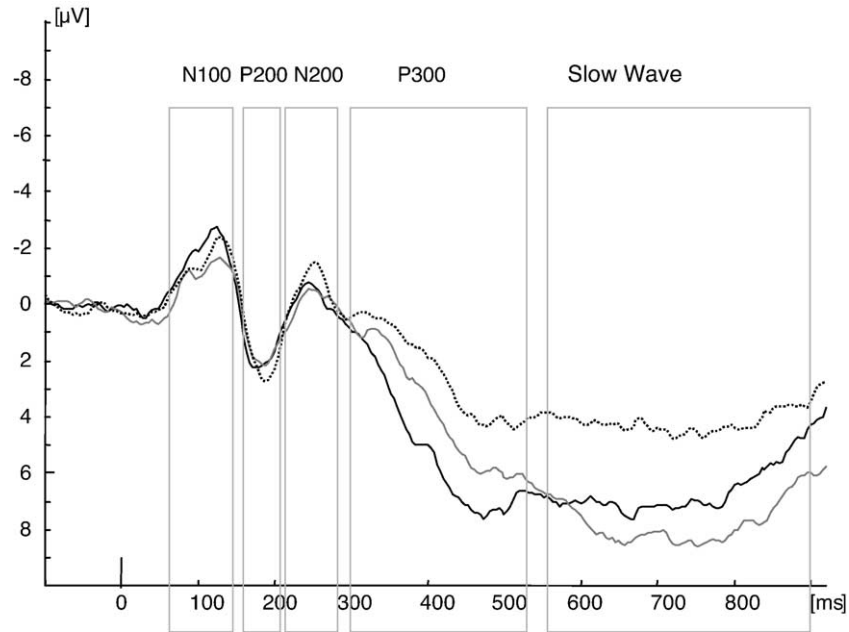
Fig. 4. Grand means ($N = 44$) of the VEPs at the electrode CZ for pleasant (black), neutral (dashed) and unpleasant (gray) slides. Note: positive is down.

posterior–superior sites revealed a discrimination between affective pictures and neutral ones, $P < 0.05$.

### 3.3.3. SLOW WAVE (550–900 ms)

In the slow wave window, a significant main effect of *Emotion Content* ($F(5, 210) = 2.20$, $P < 0.01$, $\eta^2 = 0.33$, $\varepsilon = 1.00$) was obtained, reflecting greater ERP amplitudes for unpleasant (3.58 μV) and pleasant (2.87 μV) as compared to neutral content (1.41 μV; $P < 0.05$).

A significant main effect of *Region* ($F(5, 210) = 72.25$, $P < 0.001$, $\eta^2 = 0.63$, $\varepsilon = 1.00$) indicated that medial and anterior sites, especially medial–superior and anterior–superior sites, contributed most to the positive slow wave amplitude ($P < 0.05$).

Additionally, the main effect of *Hemisphere* reflected that the mean activity in the left hemisphere was enhanced (mean amplitude 2.94 μV left vs. 2.30 μV right, $F(1, 42) = 9.00$, $P < 0.01$, $\eta^2 = 0.18$, $\varepsilon = 0.83$).
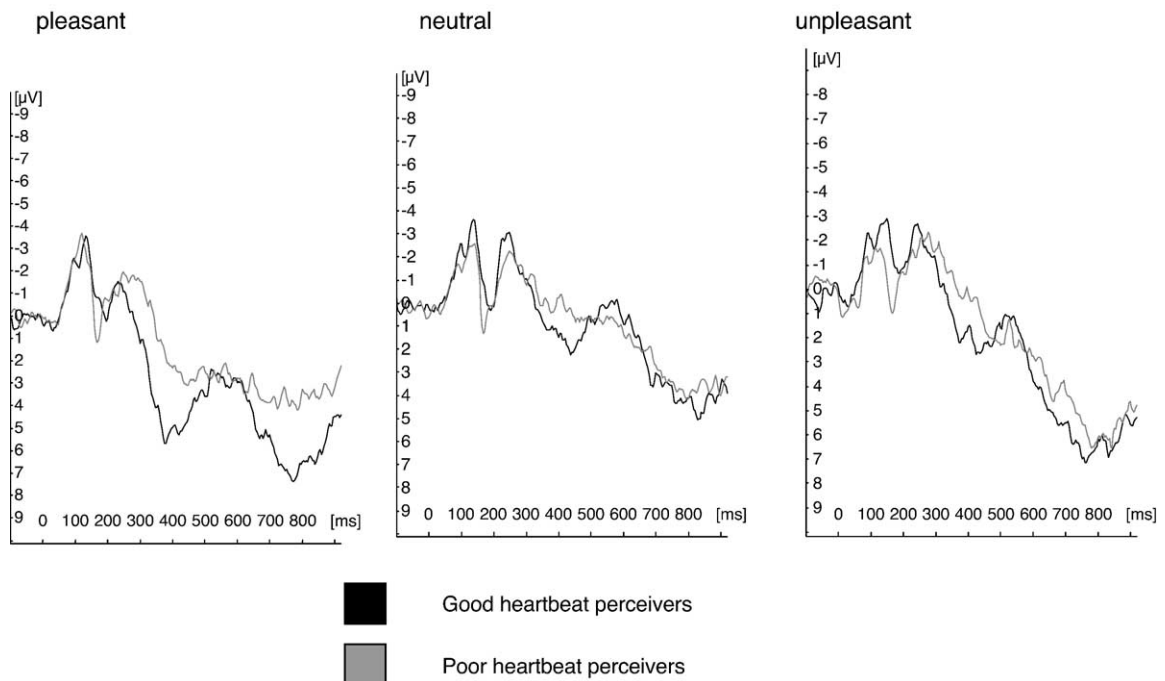


Fig. 5. VEPs of good (black) and poor (gray) heartbeat perceivers at left anterior–superior electrode site for pleasant, neutral and unpleasant slides. Note: positive is down.
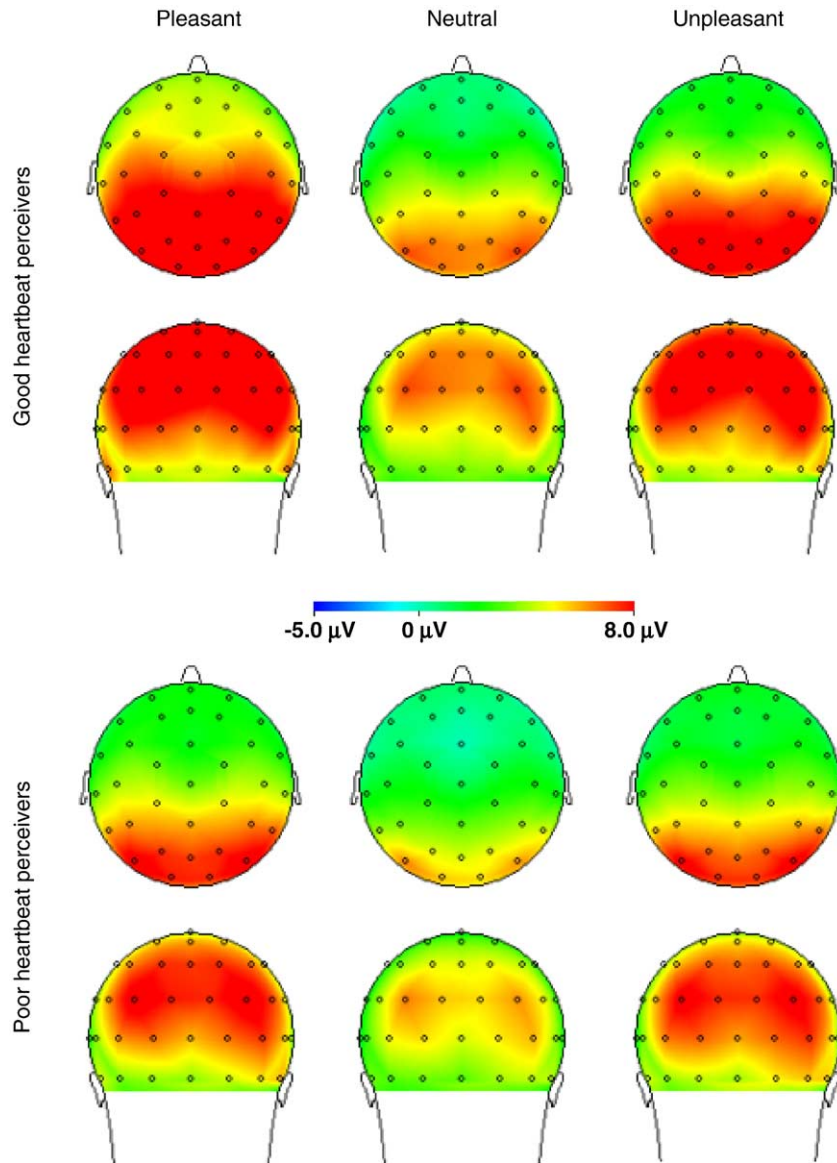
Fig. 6. Grand mean topography of the voltage distribution for the P300 latency range, contrasting good and poor heartbeat perceivers.

Furthermore, a significant *Emotion Content × Region interaction* ($F(10, 420) = 5.14$, $P < 0.001$, $\eta^2 = 0.11$, $\varepsilon = 0.99$) was obtained. All regions except for the posterior–inferior region showed an amplitude enhancement for unpleasant and pleasant slides as compared to neutral content ($P < 0.05$).

An interaction effect between *Hemisphere × Heartbeat perception* ($F(1, 42) = 5.44$, $P < 0.05$, $\eta^2 = 0.12$, $\varepsilon = 0.63$) indicated that mean activity in the left hemisphere (3.37 μV) was significantly higher than in the right hemisphere only for good heartbeat perceivers (2.22 μV), while no differences were observed in the group of poor heartbeat perceivers (2.52 μV vs. 2.38 μV).

More interestingly, mean voltage in the slow wave time window resulted in an *Emotion content × Hemisphere × Heartbeat Perception interaction* ($F(2, 84) = 3.67$, $P < 0.05$, $\eta^2 = 0.08$, $\varepsilon = 0.60$). Repeated measurement of

ANOVAs for each emotion content indicated that significant *Hemisphere × Heartbeat perception* interactions occurred only for *pleasant and unpleasant slides* ($F(1, 42) = 5.81$, $P < 0.05$, $\eta^2 = 0.12$, $\varepsilon = 0.65$ and $F(1, 42) = 6.68$, $P < 0.05$, $\eta^2 = 0.14$, $\varepsilon = 0.71$, respectively), and not for neutral ones ($F(1, 42) = 1.91$, $P > 0.5$; see Fig. 6).

For both pleasant and unpleasant pictures, significant *Hemisphere × Region × Heartbeat Perception interactions* ($F(5, 210) = 2.81$, $P < 0.05$, $\eta^2 = 0.06$, $\varepsilon = 0.68$ and $F(5, 210) = 3.09$, $P < 0.05$, $\eta^2 = 0.07$, $\varepsilon = 0.69$, respectively) were found. Post hoc Bonferroni-adjusted ANOVAs for each region demonstrated that good heartbeat perceivers showed significantly higher activation in the left hemisphere as compared to poor heartbeat perceivers at anterior and medial electrode sites ($P < 0.05$). In order to show the time course and the effect of heartbeat perception especially for the slow wave ampli-
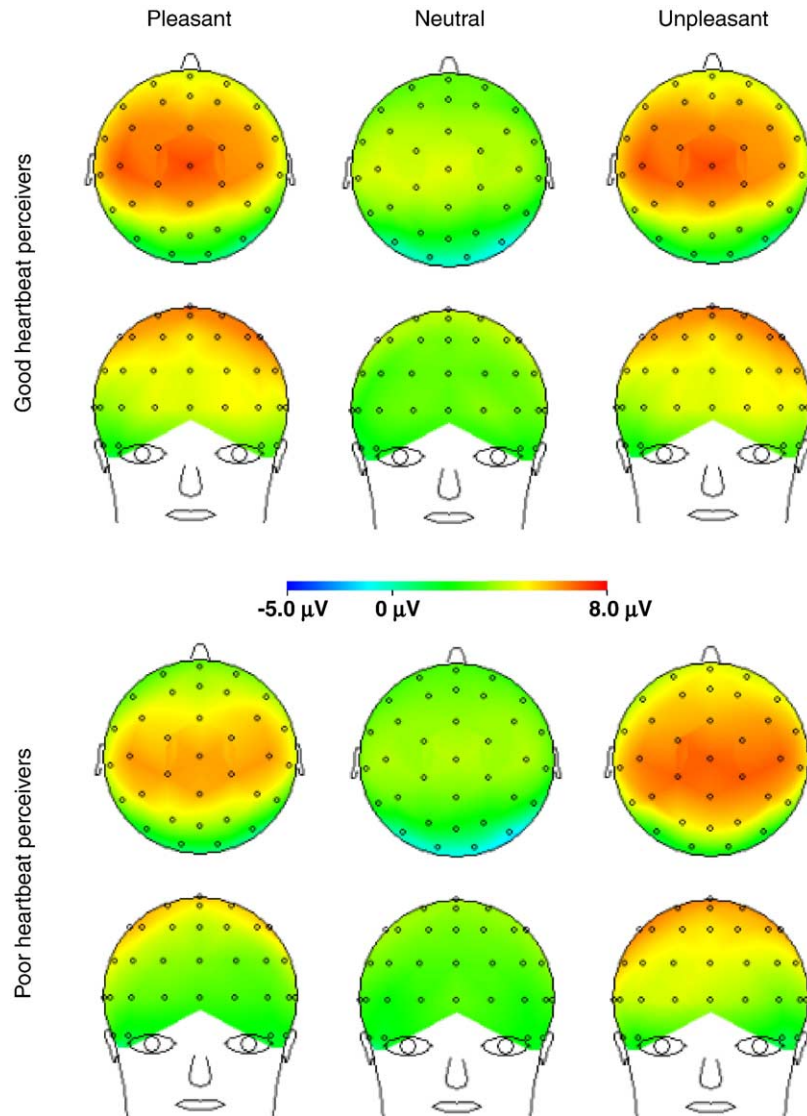
Fig. 7. Grand mean topography of the voltage distribution for the slow wave latency range, contrasting good and poor heartbeat perceivers.

tude, the left anterior–superior region with prominent differences in the slow wave amplitude between good and poor heartbeat perceivers was chosen and summarized in Fig. 4.

### 3.4. Analyses of the SAM-ratings

Fig. 8 shows the valence and arousal SAM-ratings for all three experimental conditions, separated for good and poor heartbeat perceivers.

#### 3.4.1. Valence ratings

As expected, the statistical analysis revealed a highly significant main effect for *Emotion Content* ($F(2, 78) = 351,7$; $P < 0.001$; $\eta^2 = 0.90$; $\varepsilon = 1.00$). Post hoc, Bonferroni-adjusted analyses revealed that SAM-ratings for pleasant pictures were significantly higher as compared to neutral (mean difference 2.04; $P < 0.001$) and

unpleasant slides (mean difference 4.31; $P < 0.001$). In addition, valence ratings for neutral slides were significantly higher as compared to unpleasant slides (mean difference 2.27; $P < 0.001$).

Neither the between-subject factor of heartbeat perception was significant ($F(1, 39) = 0.14$; $P < 0.05$), nor the interaction effect between valence and heartbeat perception ($F(2, 78) = 1.13$; $P < 0.05$).

#### 3.4.2. Arousal ratings

With respect to arousal ratings, a highly significant main effect of *Emotion Content* ($F(2, 78) = 245.1$; $P < 0.001$; $\eta^2 = 0.86$; $\varepsilon = 1.0$) was observed. Unpleasant pictures yielded the significantly highest arousal ratings as compared to pleasant pictures, which scored significantly higher than neutral pictures (mean 6.01 vs. 5.00 vs. 2.54; $P < 0.05$).

In addition, the between-subject factor of *Heartbeat Perception* was significant ($F(1, 39) = 5.90$; $P < 0.05$; $\eta^2 =$
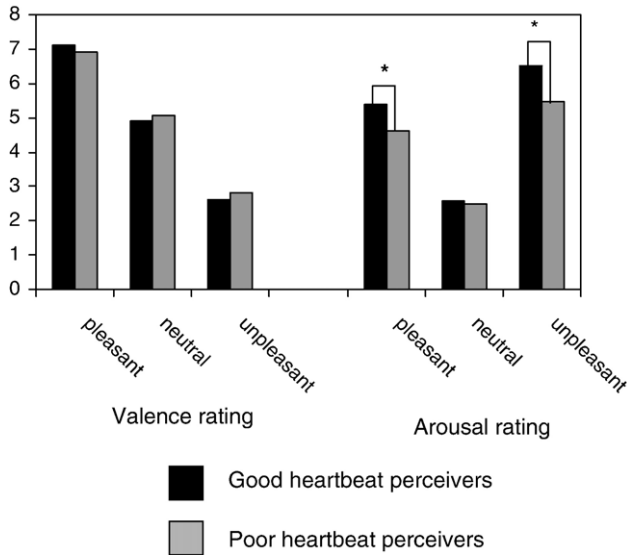
Fig. 8. Mean valence and arousal rating scores of the SAM for good (black line) and poor (gray line) heartbeat perceivers. Note: Significant differences ($P < 0.05$) are characterized by a *.



Fig. 9. Correlation between the heartbeat perception score and the mean arousal score.

0.13; $\varepsilon = 0.66$). Good heartbeat perceivers yielded higher mean arousal scores than poor heartbeat perceivers (mean 4.83 vs. 4.19).

Furthermore, a significant interaction effect of *Emotion Content × Heartbeat Perception* ($F(2, 78) = 4.54$; $P < 0.05$; $\eta^2 = 0.10$; $\varepsilon = 0.76$) was observed. Post hoc ANOVAs revealed that SAM-ratings of good heartbeat perceivers were significantly higher for pleasant and unpleasant pictures (pleasant pictures: mean 5.4 vs. 4.6; $F(1, 39) = 5.63$; $P < 0.05$; $\eta^2 = 0.13$; $\varepsilon = 0.64$; unpleasant pictures: mean 6.5 vs. 5.5; $F(1, 39) = 10.70$; $P < 0.01$; $\eta^2 = 0.22$; $\varepsilon = 0.89$), but not for neutral slides (neutral pictures: mean 2.6 vs. 2.5; $F(1, 39) = .09$; $P > 0.5$) as compared to the poor heartbeat perceivers.

### 3.5. Correlation analyses between heartbeat perception and both arousal ratings, and the mean amplitudes in the P300 and slow wave windows

#### 3.5.1. Heartbeat perception and arousal ratings

The correlation coefficient between the heartbeat perception score and the mean arousal score was significantly positive ($r = 0.34$; $P < 0.05$; see Fig. 9).

#### 3.5.2. Heartbeat perception and P300 amplitudes

In the P300 time window, we correlated the heartbeat perception score and the mean slow-wave amplitudes averaged across emotion contents. As medial and posterior sites contributed most to the P300 amplitude (see Figs. 3 and 6), we chose medial and posterior mean amplitudes, and corrected the significance level for two planned correlation analyses to $P < 0.025$. We observed positive correlations between the heartbeat perception score and medial ($r = 0.27$) as well as posterior mean
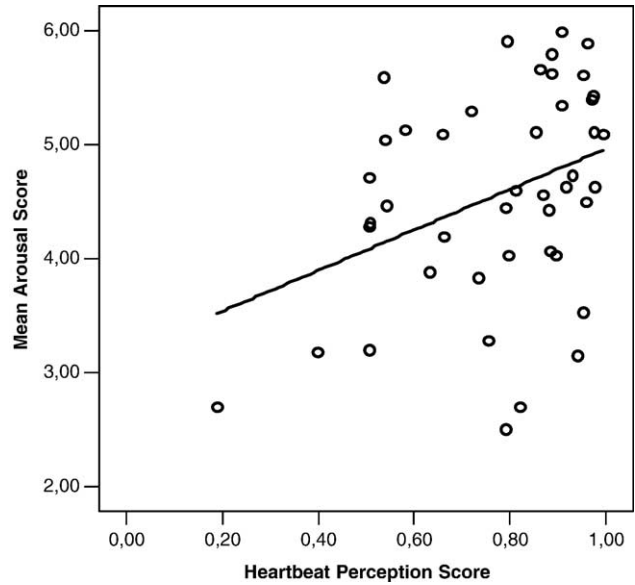
amplitudes ($r = 0.22$). However, only the correlation for medial sites reached significance ($P < 0.05$; see Fig. 10).

#### 3.5.3. Heartbeat perception and slow wave amplitudes

We correlated the heartbeat perception score and the mean slow wave amplitudes averaged across pleasant and unpleasant slides. In accordance with the ANOVA results reported above, we chose only left anterior and medial sites, and corrected the significance level for four planned correlation analyses to $P < 0.01$. We observed highly positive correlations between the heartbeat perception score and both antero-superior left ($r = 0.34$, $P < 0.01$), antero-inferior left ($r = 0.46$, $P < 0.001$) and medial–
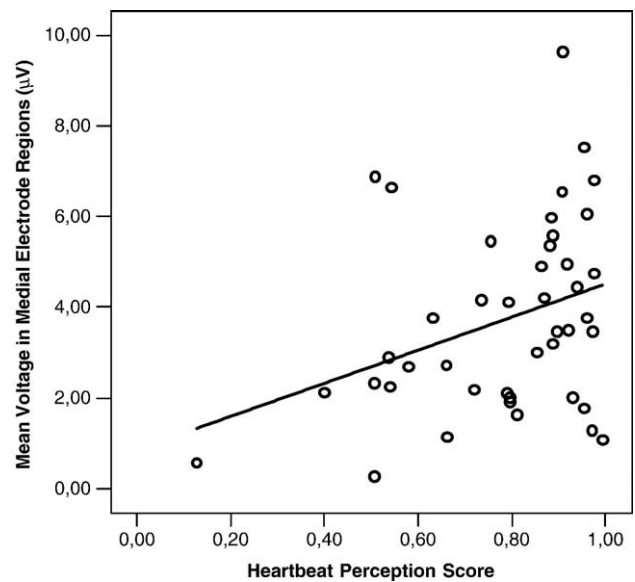


Fig. 10. Correlation between the heartbeat perception score and the mean voltage in medial electrode regions in the P300 latency range.
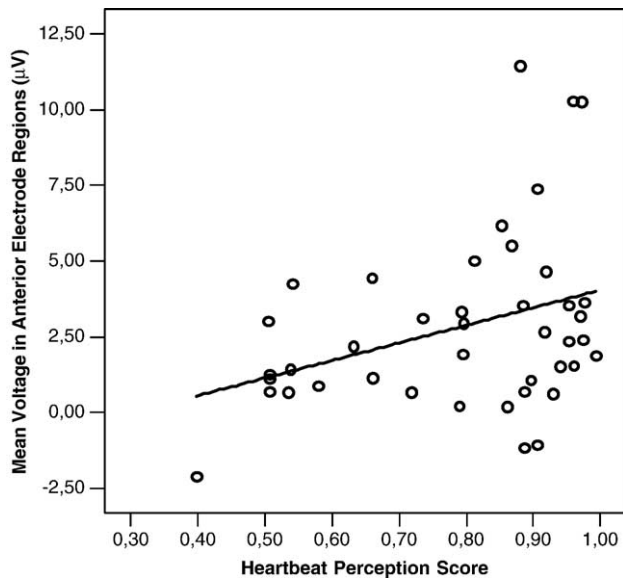
Fig. 11. Correlation between the heartbeat perception score and the mean voltage in anterior electrode regions in the Slow Wave latency range.

inferior left ($r = 0.37$, $P < 0.01$) mean amplitudes (see Fig. 11).

## 4. Discussion

In this experiment, the VEPs to emotional stimuli were recorded and analysed focussing on the role of heartbeat perception on both emotion-related brain activity and experienced emotional arousal. In accordance with our hypotheses, the ability to perceive one's heartbeats accurately had a major influence both on the VEPs and the reported arousal. Moreover, we observed significant positive correlations between the heartbeat perception score and both the mean SAM arousal rating scores and the mean amplitudes of the P300 and the slow wave.

The VEPs showed a strong dependence on the factor of emotion content. According to Cuthbert et al. [24] and Palomba et al. [59], event-related potentials started to differ among emotion contents between 200 and 300 ms after picture onset; similar to their results in the P300 region (300–400 ms), pleasant pictures prompted the greatest positivity. Both types of emotional stimuli prompted a greater positivity than neutral stimuli in the P300 latency window and in the slow wave window (compare also e.g. [24,48]). This result is in accordance with several studies [24,48,59], indicating that emotional (either pleasant or unpleasant) stimuli are more deeply processed and therefore elicit a higher level of cortical activity. One possible explanation suggests that motivationally-relevant stimuli may automatically direct attentional resources and therefore cause the observed arousal-related enhancement in the VEPs [48,55]. Especially the slow wave indicates a selective processing of emotional stimuli, reflecting a greater allocation of perceptual processing resources to motivation-

ally relevant input [47]. This assumption is confirmed by findings showing that emotional slides are rated as being more interesting and elicit longer viewing times than neutral slides [54].

As found in previous studies (e.g. [24,48,59,63]), the observed VEPs showed a significant main effect of location, with the largest positivity of the P300 amplitude over posterior sites, intermediate positivity over medial sites and the least positivity over anterior sites. It is an often-observed result that the P300 to visual stimuli is usually larger at posterior scalp sites and minimal at frontal electrodes (e.g. [50]). Both Keil et al. [48] and Palomba et al. [59] reported the largest differences in the VEPs as a function of emotional content for electrode sites near PZ. When assessing the estimated sources using a minimum norm solution, Keil et al. [48] found maximum dipole strength over posterior and parietal sites for the P300. Concerning the slow wave window, medial and anterior sites contributed most to the positive slow wave voltage in this study. This result is confirmed by Keil et al. [48] who also found activity originating at lateral–inferior and anterior regions for the slow wave when using the minimum norm source estimation.

In accordance with our hypotheses, the degree of heartbeat perception had a major influence both on the VEPs and the subjective arousal to emotional stimuli.

In the P300 time window, good heartbeat perceivers showed significantly more positive mean P300 amplitudes for all emotion contents than did poor heartbeat perceivers. Additionally, we found positive correlations at medial and posterior electrode sites of up to $r = 0.27$ for the heartbeat perception score and the mean P300 amplitudes averaged over all picture contents. The P300 is a classic index of attention, processing capacity, motivational relevance or task difficulty [50], and it has been associated with emotional arousal in previous studies. For example Polich and Kok [63] suggested that psychophysiological arousal contributes to the P300, and many studies [24,47,59] have shown an enhancement of the P300 for emotional arousing stimuli. The differences in the P300 amplitude observed between good and poor heartbeat perceivers occurred in a widespread manner, independent of the affective content and over all electrode sites, especially at posterior and central locations that contribute the most to the positive voltage of the P300. In the slow wave window, we also found significant differences between good and poor heartbeat perceivers, but only for affective slides. As compared to poor heartbeat perceivers, good heartbeat perceivers showed an enhanced mean activity in the left hemisphere for pleasant and unpleasant slides.

Extending these results, we observed for affective slides highly positive correlations between the heartbeat perception score and the mean slow wave amplitudes ranging from $r = 0.34$ for the antero-superior left electrode site to $r = 0.46$ at the left antero-inferior electrode site. Consistent with our results, Cuthbert et al. [24] showed that late positive

potentials (e.g., 700–1000 ms) are specifically enhanced for pictures that are more emotionally intense (i.e., those described by viewers as being more arousing). Keil et al. [47] also showed a modulation of late positive ERPs as a function of emotional arousal. Our results suggest that perceptual differences in interoceptive awareness are reflected in late positive ERP components to emotional stimuli, since heartbeat perception has a major influence on both the P300 and the slow wave amplitudes. Congruent to our interpretation, Kok [50] assumes that the positive slow wave and P300 components present similar processes, as reflected by a greater allocation of perceptual processing resources to motivationally relevant input. While we found a main effect of heartbeat perception for all emotion contents in the P300 time window, differences between good and poor heartbeat perceivers in the slow wave window were only present for affective slides and were lateralized to some extent. Enhanced slow wave amplitudes for good heartbeat perceivers were present over the left hemisphere. Former research partly supports this lateralization. For example, Smith et al. [76] showed higher brain electrical activity in the left hemisphere under emotional stimulation. Similarly, Waldstein et al. [84] reported more prominent left EEG activation in happiness-inducing tasks, whereas anger-inducing tasks were associated with left and right frontal EEG activation levels. In a review of the empirical literature on central nervous system and autonomic nervous system concomitants of emotional states, Hagemann et al. [37] point out that neuroimaging studies generally tend to show left activation through emotional arousal which also confirms our results.

As reported above, we found considerable differences in the P300 and slow wave amplitudes in relation to heartbeat perception. Many subcortical and cortical structures are engaged in visceral processing, and growing evidence supports the engagement of four cortical structures in visceroception, namely the anterior cingulate, the medial prefrontal cortex, the insula and the somatosensory cortex (see e.g., Cameron, 2001). Concerning the slow wave latency range, the most prominent differences between good and poor heartbeat perceivers appeared at left superior–anterior region. Activity recorded over this region may be generated in the anterior cingulate and the medial prefrontal region [3,32,61,65,68,69,80,90]. Damasio et al. [28] demonstrated that structures relevant for visceral regulation and homeostasis, such as the insular cortex, the somatosensory cortices, the anterior and posterior cingulated cortices, are engaged in all emotional processing. Confirming this assumption, many studies investigating the neural basis of emotions have shown that the prefrontal cortex, the anterior cingulated, the insula and the amygdala are implicated in aspects of human emotion [5,7,13,15,19,21,26,51,52,66,81,79]. Thus, the observed differences between good and poor heartbeat perceivers in the P300 and slow wave latency ranges could be explained by different activation patterns in those cortical areas concerned with both emotional processes and visceral regulation. As our

results in the P300 latency range yielded over posterior and medial sites the most prominent differences between good and poor heartbeat perceivers, occipital, parietal or medial frontal structures have to be considered as generators for this activity. Studies aiming to detect the generators of the P300 revealed an activation of multiple structures [3,32,80,90]. Yamazaki et al. found dipoles, in the frontal cortices [90]. Anderer et al. [3] also located P300 generators predominantly in the frontal cortex and less pronounced in the parietal cortex, while Keil et al. [48] reported maximum dipole strength over posterior and parietal sites. Our data could indicate that good heartbeat perceivers show a stronger activation in the somatosensory cortices or in the medial frontal cortex, which are structures contributing to both emotional and visceral processing. Concerning the slow wave window, good heartbeat perceivers had enhanced amplitudes at anterior and medial sites, suggesting different and stronger activation patterns at frontal and parietal structures. In accordance with our assumption Keil et al. [48] found that slow wave activity was originating at lateral–inferior and anterior regions. Again, one might assume that good heartbeat perceivers are more strongly activated in the medial frontal cortex, the anterior cingulated or the somatosensory cortices, which are structures contributing to both emotional and visceral processing.

For the N100 amplitude, we observed an enhanced activity for pleasant pictures as compared to unpleasant slides. This finding is in accordance to earlier ERP work [42,47,62] showing an enhanced activation for aversive stimuli. We did not find an effect of interoceptive awareness on the N100 amplitude. Thus, one might speculate that an interaction of emotion processing and interoceptive awareness takes place on a later stage level of stimuli processing Following the model of Damasio [27], an emotional object either derived from the environment or recalled from memory first causes activation in so-called emotion trigger sites (ventromedial prefrontal cortex, amygdala, brain stem nuclei, hypothalamus and basal forebrain) which induce changes towards the body and subsequent brain regions including first-(insula, somatosensory cortex) and second-order (anterior cingulate, prefrontal cortices) structures. As interoceptive awareness does not influence the early response in the ERP, our results suggest that converging structures for both emotion processing and interoception are probably first and second-order structures, an assumption confirmed by studies identifying possible sources of the P300 [3,32,80,90].

In this context, it is of importance that good heartbeat perceivers reported significantly higher arousal to emotional stimuli. This finding is in accordance with the study of Wiens et al. [89], where good heartbeat perceivers rated emotional film clips as more intense than poor heartbeat perceivers. In our study, good heartbeat perceivers showed both an enhancement of the P300 and the slow wave amplitudes, as well as higher levels of reported arousal to pleasant and unpleasant slides. Moreover, we found a

positive correlation of $r = 0.34$ between the heartbeat perception score and the mean arousal score. Heartbeat perception ability is positively related to reported arousal in an emotional stimulation setting, and – as reported above – also positively correlated to the EEG mean amplitudes in the P300, as well as in the slow wave range. Taking these results together, one can assume that the observed differences in the VEPs are partly mediated by differences in the arousal levels of good and poor heartbeat perceivers in an emotional setting. Consistent with this interpretation, Cuthbert et al. [24] reported a significant positive correlation of 0.27 between the arousal ratings and the EEG voltage in the slow wave window (700–1000 ms). One might ask whether the interaction between arousal and heartbeat perception is independent of stimulus content, however some evidence exists which supports the view that the described arousal effects occur during the processing of emotions. Consistently, the reported arousal scores for neutral slides did not differ between good and poor heartbeat perceivers.

Our results provide support for those theories of emotion processing, which state that perceived visceral activity affects experienced emotion [6,20,25,27,40]. As heartbeat detection correlates with the ability to detect changes in other autonomically innervated organs [88], the categorization in good versus poor heartbeat perceivers should reflect a general sensitivity for visceral processes. Our results confirm this assumption, suggesting that the ability to perceive one's heartbeats accurately is an index for sensitivity to visceral cues that occur in stimulation with emotional stimuli such as changes in bodily states. The perception of changes in bodily states is associated with a higher level of emotional arousal, which is reflected in both emotion-related brain activity and reported intensity of emotions. Good heartbeat perceivers may react with an augmented affective arousal due to a more precise perception of their heartbeats in the experimental situation. In accordance with our assumption, Katkin et al. [46] showed that the ability to detect one's heartbeats correctly was related to better performance in a fear-conditioning experiment. They suggested that good heart-beat perceivers used the perception of visceral cues from the conditional fear response to facilitate the prediction of shocks. One can hypothesize that a deficit in perceiving visceral cues may be associated with deficits in emotional processing. This interpretation is confirmed by Kayser et al. [44] who observed reduced P300 amplitudes during emotional processing in depression. They suggested that an enhancement of late positivity to emotional significant stimuli may function as a somatic marker, required for guiding individual behaviour by signalling stimulus significance to the body (compare [25,28]). In this context, one might speculate that the observed differences in the VEPs between good and poor heartbeat perceivers are related to different activation patterns in structures coordinating emotional and visceral information like the anterior cingulated, the medial frontal gyrus and the somatosensory cortices or the insula [14,28]. The topographic distribution of the voltage differences in the P300 and slow wave amplitudes, namely most prominent at medial and frontal sites, would allow such an assumption.

## Acknowledgment

## Appendix A

Pleasant pictures used were: 1590, 2050, 2080, 2150, 2311, 2341, 4610, 4652, 4659, 4660, 4664, 4670, 4680, 5600, 5830, 7230, 7350, 8080, 8200, 8510.

Unpleasant pictures used were: 1050, 1090, 1110, 1120, 1200, 1220, 1300, 3100, 3140, 6200, 6350, 6510, 6540, 6610, 9000, 9010, 9050, 9160, 9190.

Neutral pictures used were: 2190, 2210, 2480, 2850, 5500, 5520, 6150, 7009, 7020, 7040, 7050, 7060, 7080, 7090, 7100, 7130, 7150, 7175, 7190, 7235.

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