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NeuroImage 37 (2007) 663–673

Hemodynamic brain correlates of disgust and fear ratings

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Received 24 November 2006; revised 3 May 2007; accepted 8 May 2007
Available online 22 May 2007

Inconsistent findings from several functional magnetic resonance imaging (fMRI) studies on fear and disgust raise the question which brain regions are relatively specialized and which are general in the processing of these basic emotions. Some of these inconsistencies could partially be due to inter-individual differences in the experience of the applied emotional stimuli. In the present study, we therefore correlated the participants' individual online reports of fear and disgust with their hemodynamic responses towards each of the fear- and disgust-inducing scenes.

Sixty six participants (32 females) took part in the fMRI study. In an event-related design, they saw 50 pictures with different emotional impact (10 neutral, 20 disgust-inducing, 20 fear-inducing). Pictures were presented for 4 s and participants rated each picture online – just after the presentation – on the dimensions disgust and fear among others.

The results indicate that the processing of disgust- and fear-inducing pictures involves similar as well as distinct brain regions. Both emotional stimulus categories resulted in activations in the extended occipital cortex, in the prefrontal cortex, and in the amygdala. However, insula activations were only significantly correlated with subjective ratings of disgust, pointing to a specific role of this brain structure in the processing of disgust.

Introduction

There is an ongoing debate which neural substrates are specific in the processing of the basic emotions fear and disgust and which have a more general role. The reviews by Calder et al. (2001) and Murphy et al. (2003) report that the insular cortex and the basal ganglia were more frequently activated during disgust processing than during fear processing while amygdala was more frequently activated in fear processing. This implicates that the neural mechanisms underlying disgust and fear might be separate in part. Murphy et al. (2003) and Phan et al. (2002) identified brain regions like the medial frontal cortex and the visual cortex responding to emotional stimuli in general.

Rolls (1999) assumes in his model that limbic structures – especially the amygdala – together with orbitofrontal areas are responsible for the evaluation of the reinforcement value of stimuli. Neural re-projections to primary and secondary sensory cortices ensure that salient stimuli are optimally processed (Amaral et al., 1993), resulting, in the case of visual stimuli, in increased neural activations in primary and secondary visual areas. Recent results of several fMRI studies in our research group using pictures of emotional scenes as stimuli in different experimental designs are in line with such integrative models of emotion. We were able to demonstrate that a set of different regions including the occipital–temporal cortex (OTC) and the amygdala are active during the processing of both fear and disgust (Schienle et al., 2002a, 2005, 2006; Stark et al., 2003, 2005).

However, the role of the insula within this network remains unclear. Schienle et al. (2005, 2006) and Stark et al. (2003, 2004) found insula activation neither under fear-eliciting nor disgust-inducing stimulation, while Schienle et al. (2002a) and Schäfer et al. (2005) detected insula activation in *both* fear and disgust conditions. Mathews et al. (2004) found increased activation in both insula and amygdala in response to fear-related vs. neutral pictures. In contrast, Wright et al. (2004), using pictures of disgusting scenes, reported insula activation to be disgust-specific.

Some of these inconsistencies, we hypothesize, could be due to inter-individual differences in the experience of emotional stimuli. Most of the fMRI studies mentioned above used block designs, i.e. the emotional stimuli were presented in homogenous blocks of the same category (e.g. Schienle et al., 2006; Wright et al., 2004). The brain activation towards highly intense emotional stimuli is thereby contrasted with the activation towards blocks of neutral stimuli. Such an approach does not consider individual differences in the reactions to the emotional stimuli, even if participants have to rate the stimuli after the experiment. These post hoc ratings are usually not included into the statistical model but only used to verify the a priori assigned emotional categories. Post hoc ratings can further be problematic because they are subject to memory and habituation effects. Therefore, it seems appropriate to rate the stimuli immediately after each

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Available online on ScienceDirect (www.sciencedirect.com).

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doi:10.1016/j.neuroimage.2007.05.005

presentation. Individual ratings can then be entered into the statistical analyses instead of using a priori assignments.

Heinzel et al. (2005) followed this approach using visual emotional stimulation with pictures of emotional scenes. They showed that functional activations in the orbitofrontal and dorsomedial prefrontal cortex, as well as in the medial parietal cortex and the insula were significantly correlated with the subjective ratings of emotional valence (ranging from positive to negative). Anders et al. (2004) investigated the relationship between different emotional response systems (subjective ratings, electrodermal responses, startle reflex) and functional brain activation in a picture perception paradigm. Starting from the two dimensions of the verbal emotional space, valence (positive vs. negative) and arousal (high vs. low), they found that subjective ratings of negative valence ("unpleasant") correlated with the activation of the insula. The arousal ratings of the pictures were significantly related to thalamic activation. Yet, these studies did not aim at a comparison of specific emotions but used emotion unspecific dimensions like valence or arousal for correlation with the fMRI data.

In the present study we directly compared the neural correlates of the basic emotions fear and disgust in an event-related picture perception paradigm. That is, we did not present the pictures in homogenous blocks of the same emotional category and intensity but in single trials with a randomized order of pictures. These pictures covered a broad range of emotional intensities. We measured the subjective ratings in this parametric design online, directly after each picture presentation. We presumed that the inclusion of the subjective ratings into the statistical analyses would help to improve the detection of possible differences and similarities in fear- and disgust-related brain activations. The study also allowed comparing the results of this parametric approach with those of a classical categorical fear vs. disgust contrast.

Materials and methods

Participants

Sixty-six healthy right-handed participants took part in the study (34 males, 32 females). They were 19 to 44 years old (mean age: 24.7 years, SD = 5.2) and most of them were students, who received either course credits or were paid (15 Euros) for their participation. None of them was taking regular medication or had a previous history of psychiatric or neurological treatment. The study was performed in accordance with the ethical standards established in the fifth revision of the Declaration of Helsinki and approved by the Ethical Committee of the German Society of Psychology.

Stimuli material

During the fMRI session, which lasted 32 min, the participants were presented 10 pictures typically rated as emotionally neutral (NEUTRAL), 20 pictures typically rated as disgust-inducing (DISGUST) and 20 pictures, which are typically rated as fear-inducing (FEAR). The content of the fear and the disgust pictures varied in intensity. Most of the neutral and fear-inducing pictures were taken from the International Affective Picture System (IAPS, Lang et al., 1999, picture numbers — neutral: 1450, 1740, 2745.1, 7010, 7135, 7235; disgust: 9570; fear: 1300, 1302, 1560, 5940, 5972, 6212, 6230, 6312, 6313, 6350, 6370, 6510, 6560, 9910); the remaining pictures were collected by the authors. The disgust-inducing pictures represented a broad range of different disgust elicitors: disgusting animals (e.g. black beetles), physical deviations/death (e.g. eczema, cadavers), poor hygiene (e.g. dirty toilet), unusual or rotten food (e.g. man eating a grasshopper, bread with mildew), and body products (e.g. excrements). Fear-inducing pictures showed threatening situations either through attacks by animals (e.g. sharks, lions), attacks by humans (e.g. with knives or pistols), or disasters (e.g. fire, car accident). The neutral pictures displayed animals (e.g. duck, eagle, owl), furniture (e.g. chair, lamp), and everyday life scenes with one or more persons. Pictures of the three categories were comparable with regard to depicted humans and physical features like complexity or color. An LCD projector (model EPSON EMP-7250) projected pictures onto a screen at the end of the scanner (visual field = 18°). These were viewed through a mirror mounted to the head coil. All pictures had an 800 × 600 pixel resolution.

Self report data

Participants rated the pictures on the dimensions valence, arousal, fear, disgust, and implied motion just after their presentation using a three-button keypad. Participants saw 9 rectangles – representing a 9-point scale – on the screen. At the beginning of each rating the fifth (middle) box was marked. Then, the participants could move the mark with the left button to the left and with the middle button to the right. When the marked box corresponded to their intended response, the right button was used to confirm the answer. The rating scales were presented in sequence, always in the same order: valence, arousal, disgust, fear, and implied motion. The implied motion rating ('How much movement do you associate with this picture?'; a picture of a flying duck was normally rated as high, a picture of a chair was rated as low in implied motion) was introduced because we had previously observed activation differences in the secondary visual fields between disgust and fear pictures (Stark et al., 2004; Schäfer et al., 2005). We assume that this could at least be partly explained by differences in the implied motion of the pictures. The according analyses are beyond the scope of this study and will be reported separately.

For the valence and arousal ratings a computerized version of the Self Assessment Manikin (SAM; Bradley and Lang, 1994; 9-point scale) was applied, the other ratings consisted of questions (e.g. 'How much disgust did you experience during the picture presentation?') to which an agreement between 'not at all' to 'very much' had to be given on the 9-point scale. The time for each rating was limited to 5 s. When participants did not finish their ratings within this interval, the experiment continued and the rating data were labeled as missing.

After the experiment, each participant filled in two trait questionnaires concerning disgust and anxiety. The Questionnaire for the Assessment of Disgust Sensitivity (QADS; Schienle et al., 2002b) assesses participants' general proneness to disgust (trait disgust). The self-rating instrument describes 37 disgust-related situations, which have to be judged on a 5-point scale (0 = 'not disgusting'; 4 = 'very disgusting'). Participants also filled in the trait scale of the State Trait Anxiety Inventory (STAI; Laux et al., 1981), stating how often they generally experience 20 specific fear-related feelings on a 4-point scale. The range of possible sum scores varies between 20 and 80.

Skin conductance responses

Skin conductance responses (SCR) were continually registered during the experiment inside the scanner. SCR was measured by

means of a custom-made device (sampling rate: 10 Hz) using standard Ag/AgCl electrodes (diameter: 8 mm) filled with isotonic (0.05 M NaCl) electrolyte medium, placed hypothenar at the left hand. When the skin conductance increased more than 0.05 μs within a time window of 1 to 5 s after picture onset, a response was scored. A logarithmic transformation was conducted to ensure comparability between the participants.

Imaging and analyses

Brain images were acquired using a 1.5 T whole-body tomograph (Siemens Symphony) with a standard head coil. Structural image acquisition consisted of 160 T1-weighted sagittal images (MPRage, 1 mm slice thickness). For functional imaging a total of 620 volumes were registered using a T2*-weighted gradient echo-planar imaging sequence (EPI) with 32 coronal slices covering the whole brain (slice thickness = 5 mm; 1 mm gap; descending; TR = 3.1 s; TE = 55 ms; flip angle = 90°; field of view = 192 mm × 192 mm; matrix size = 64 × 64). The slices were initially aligned parallel to the AC–PC line and then additionally tilted 90°.

The statistical parametric mapping software package (SPM2, Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab (Mathworks, Inc., Natick, MA, USA, release 13) was used for preprocessing and statistical analyses. Origin coordinates were adjusted to the anterior commissure (AC), and realignment (third order B-spline), slice time correction, and normalization to the standard brain of the Montreal Neurological Institute (MNI) were performed. Smoothing was executed with an isotropic three-dimensional Gaussian filter with a full width at half maximum (FWHM) of 9 mm.

For the event-related design, each picture presentation was modeled with a box-car function convolved with a hemodynamic response function (duration 4 s) in the General Linear Model of SPM. The six movement parameters of the rigid body transformation applied by the realignment procedure were introduced as covariates in the model. The serial correlation in the voxel-based time series was considered as a first order autoregressive process. A high pass filter (time constant = 300 s) was implemented by using cosine functions in the design matrix.

Within the conventional categorical analysis, four T-contrasts were calculated for each participant: DISGUST > NEUTRAL, FEAR > NEUTRAL, DISGUST > FEAR, FEAR > DISGUST.

The parametric analysis – the main focus of the study – directly relates the hemodynamic responses towards the pictures to the subjective picture ratings collected after each presentation. We therefore included the subjective ratings of fear and disgust as regressors in a parametric statistical model. Significant *T*-values indicate the brain regions in which the functional activation correlates significantly with the subjective ratings independent of the a priori classification of the pictures. As fear and disgust ratings were simultaneously added as regressors to the parametric statistical model, it was possible to evaluate the influence of disgust ratings, fear ratings as well as the contrasts DISGUST > FEAR and FEAR > DISGUST.

For a random effect analysis the individual contrast images were analyzed in a second level analysis. Multiple comparison corrections were performed according to the random field theory for the whole brain ($\alpha = 0.05$).

Additionally, we focused on the amygdala, the insula, and the basal ganglia as regions of interest (ROI) because of their assumed specific role in disgust and fear processing. The ROI were defined by the anatomical parcellation of the normalized brain (single-subject high-resolution T1 volume of the Montreal Neurological Institute) as described by Tzourio-Mazoyer et al. (2002). The software MARINA (Walter, 2002) was used for creating the appropriate masks. For the statistical analysis we used the small volume correction implemented in SPM ($\alpha = 0.05$, corrected for the ROI).

Statistical analyses of the subjective data and the SCR were conducted with the statistical software package SPSS for Windows (Version 11.0, SPSS Inc. Illinois, USA). Analyses of variance (ANOVA) were conducted with the picture categories as a repeated measures factor. For all statistical analyses α was set to 0.05.

Procedure

After the experimental briefing (explanation of the study, written consent, and clarification of possible contraindications), participants trained the picture rating procedure on a computer outside the scanner using a three-button keypad. The time course of the training trial outside was identical to the trial inside the scanner. Each trial lasted 37.2 s and consisted of five phases: first, a fixation cross was presented between 0 and 3.1 s (jitter); then a picture was presented for 4 s. In a third phase, question marks overlapped the picture to signal the participants that they could terminate the presentation by pressing a button. When participants did not press the button the picture disappeared after a further 4 s. The time from the beginning of the additional presentation time, until participants pressed a button, was registered as viewing time. During the fourth phase, participants rated the pictures on the dimensions valence, arousal, fear, disgust, and implied motion. In the last phase, a fixation cross was displayed until the next trial started. Once participants were familiar with the rating procedure, they were placed into the scanner and a structural MRI was conducted.

Then, more training was carried out to get participants comfortable with the rating procedure in the scanner environment (i.e. the scanner noise and participants could not see the touchpad but only touch the buttons). If necessary, this could be repeated until participants reported sufficient familiarity with the procedure. None of the pictures used in the training session was used in the actual experiment, which included 50 pictures altogether. The order of the pictures was random, with the restriction of no more than three successive pictures from the same category. The picture sequence differed from participant to participant.

This was followed by another short experiment (7 min) showing moving dots. This was done to determine the area V5/MT individually. This region is thought to be involved in the processing of implied motion (Kourtzi and Kanwisher, 2000). Afterwards, outside the scanner, participants had to rank the disgust pictures on the dimension of disgust and the fear pictures on the dimension of fear. This task was used to identify implausible ratings given during the experiment.

Results

Subjective ratings, skin conductance, and viewing time

The analyses of variance revealed significant differences between the picture categories in all variables (all *F*-values > 6). As expected, the fear- and disgust-inducing pictures were rated as more negative in valence (FEAR-NEUTRAL, valence: $D = 2.87$, SE = 0.14, $p < 0.001$; DISGUST-NEUTRAL, valence: $D = 2.69$, SE = 0.14, $p < 0.001$) and more arousing (FEAR-NEUTRAL, arousal: $D = 3.41$, SE = 0.16,

$p<0.001$; DISGUST-NEUTRAL, arousal: $D=1.99$, SE=0.14, $p<0.001$) than the neutral pictures. They were also rated as more fear- (FEAR-NEUTRAL, fear rating: $D=4.61$, SE=0.21, $p<0.001$; DISGUST-NEUTRAL, fear rating: $D=1.18$, SE=0.13, $p<0.001$) and disgust-inducing (FEAR-NEUTRAL, disgust rating: $D=1.35$, SE=0.13, $p<0.001$; DISGUST-NEUTRAL, disgust rating: $D=4.79$, SE=0.16, $p<0.001$), respectively. The fear pictures were rated as slightly more negative in valence (FEAR-DISGUST, valence: $D=0.17$, SE=0.08, $p=0.03$) and more arousing (FEAR-DISGUST, arousal: $D=1.41$, SE=0.12, $p<0.001$) than the disgust pictures. Furthermore, the fear pictures received higher fear ratings than the disgust pictures (FEAR-DISGUST, fear rating: $D=3.43$, SE=0.19, $p<0.001$) and the disgust pictures received higher disgust ratings than the fear pictures (DISGUST-FEAR, disgust rating: $D=3.44$, SE=0.17, $p<0.001$). In addition, the emotional pictures triggered stronger SCR than the neutral pictures (FEAR-NEUTRAL, SCR: $D=0.05$, SE=0.02, $p=0.002$; DISGUST-NEUTRAL, SCR: $D=0.03$, SE=0.01, $p=0.04$), without differences between fear and disgust. Finally, the viewing time for the emotional pictures was longer than for the neutral pictures (FEAR-NEUTRAL, viewing time: $D=181.29$, SE=60.53, $p=0.004$; DISGUST-NEUTRAL, viewing time: $D=161.48$, SE=59.41, $p=0.01$). Fear and disgust pictures did not differ in viewing time (see Table 1). Finally, on the individual level fear and disgust ratings correlated between −0.57 and 0.89. However, the correlation coefficients were significant ($p<0.05$) only for 17 out of 66 participants. The mean of the correlation coefficients was −0.05 (SD=0.28).

Participants obtained the following questionnaire scores: QADS: $M=2.26$, SD=0.57; STAI: $M=37.50$, SD=8.90. These mean scores are comparable to those of the healthy samples with which the questionnaires had originally been validated (Schienle et al., 2002b; Laux et al., 1981).

fMRI data

Parametric modulation of the BOLD response by the subjective ratings of the pictures

Fig. 1 gives an overview of the brain activations which were significantly related to the subjective ratings of disgust and fear; i.e. the more disgust or fear the participants experienced, the stronger the functional activation in the respective brain regions. Furthermore, Fig. 1 displays those regions whose relationship to the disgust ratings was significantly stronger than to the fear ratings and vice versa. In Table 2 the activated clusters are listed in detail. Fig. 2 depicts the relationships between neural activation and disgust and fear ratings, respectively for the following regions of interest: amygdala, insula and basal ganglia.

Table 1
Means (standard deviations) of the subjective ratings and physiological responses for the three picture categories NEUTRAL, DISGUST, and FEAR

	Picture categories		
	NEUTRAL	DISGUST	FEAR
Subjective ratings			
Valence [1…9]	5.97^{c} (0.89)	3.28^{b} (0.78)	3.11^{a} (0.69)
Arousal [1…9]	2.18^{a} (1.0)	4.17^{b} (1.47)	5.59^{c} (1.59)
Disgust [1…9]	1.24^{a} (0.40)	6.03^{c} (1.42)	2.59^{b} (1.30)
Fear [1…9] $N=66$	1.23^{a} (0.39)	2.41^{b} (1.31)	5.83^{c} (1.84)
Skin conductance [log μs] $N=55$	0.11^{a} (0.14)	0.14^{b} (0.17)	0.16^{b} (0.17)
Viewing time [ms] $N=54$	1092.23^{a} (424.60)	1253.71^{b} (465.94)	1273.51^{b} (503.15)

Different subscript letters indicate variables that differ significantly between the picture categories ($\alpha=0.05$).

Disgust. The whole brain analysis for disgust generated nine activation clusters (four bilateral and one unilateral). The first two clusters comprised parts of the inferior temporal and fusiform gyri. The second pair of clusters had its activation peaks in the insula, the amygdala, and parts of the hippocampus. The third and fourth bilateral activation clusters were located in the supramarginal gyri and the middle occipital gyri. Finally, activation in the right medial orbitofrontal cortex was positively related to disgust ratings.

The ROI analyses revealed significant correlations of the disgust ratings within all regions of interest (bilateral insula, amygdala, and basal ganglia; Table 3).

Fig. 3 gives a single-subject example for the parametric approach: for each picture, the signal change in the insula is related to the disgust rating.

Fear. Whole brain analyses showed significant correlations of the rated amount of fear with activations in seven clusters. Beside a right prefrontal activation, and activation in the middle/posterior cingulate and precuneus, further bilateral activations were observed in the fusiform gyrus, the superior occipital gyrus and the middle temporal gyrus.

For the ROI, only the right amygdala showed a significant activation (Table 3).

Disgust vs. Fear. Despite a substantial amount of overlap in occipital and limbic structures (see Table 2), the fear- and disgust-related brain activation had different activation foci. While activation of the insula, the inferior temporal gyrus, the fusiform gyrus, the middle occipital gyrus, and the calcarine fissure was only associated with the disgust ratings, the fear ratings were exclusively correlated with activations in the middle frontal gyrus, the superior frontal gyrus, the middle temporal gyrus, the precuneus/posterior cingulate cortex, and occipital regions.

The ROI analyses revealed that the activation of the amygdala, the insula, and parts of the right basal ganglia correlated significantly stronger with disgust than with fear ratings. However, parts of the right basal ganglia were also significantly correlated for the contrast FEAR>DISGUST (Table 3).

To ensure that the results of the parametric analyses were not due to the neutral pictures with lowest disgust and fear ratings, analyses were also conducted without including the neutral pictures into the parametric modulation. No major differences emerged. We report only the analyses including the neutral pictures because only then a direct comparison between the parametric and categorical analyses is possible. The results of the additional analyses are available on request.

Comparison of parametric and categorical analyses

Besides the parametric analysis, incorporating the individual ratings of each picture into the statistical model, the fMRI data were analyzed in a traditional categorical way contrasting fear and disgust pictures with neutral ones (based on an a priori assignment). Since a direct comparison of the two approaches within a statistical model is not valid – due to the different data basis –

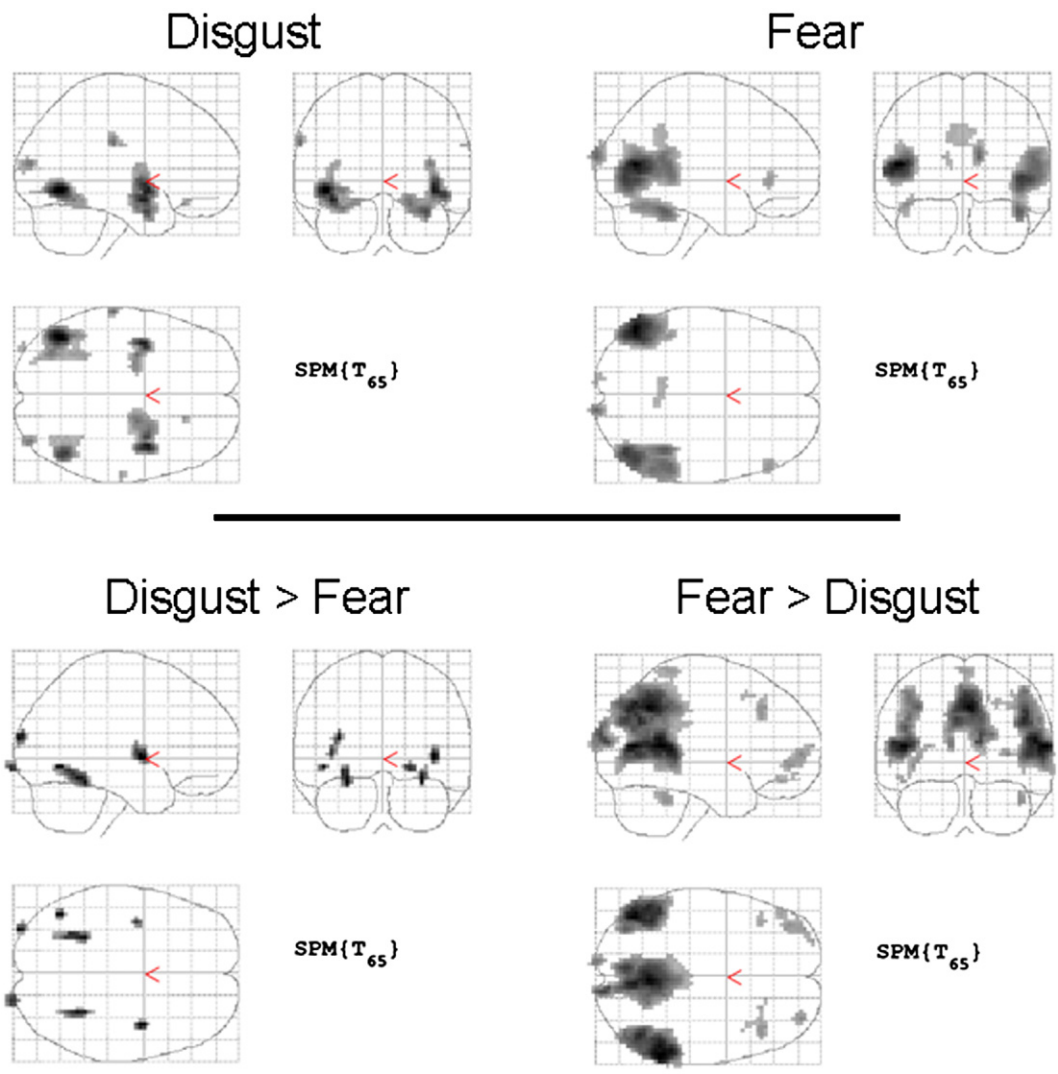

Fig. 1. Parametric analysis: activated voxels ($p<0.05$, whole brain corrected, cluster size ≥ 5) for the contrasts DISGUST, FEAR, DISGUST>FEAR, and FEAR>DISGUST in a random effect analysis. On the first level fear and disgust ratings were added as parametric regressors to the statistical model.

only a descriptive comparison is possible. The conventional categorical analysis revealed an activation pattern which was similar to the parametric modulation activation pattern, as shown in Fig. 4 and Table 4. That is, the brain regions more strongly activated during the presentation of the disgust pictures than pictures with neutral content also tended to show a significant correlation with the disgust ratings. The same applies to the fear-eliciting pictures.

Interestingly, using the categorical approach, insula activation was observed in the FEAR>NEUTRAL as well as in the DISGUST>NEUTRAL contrast (ROI analyses; Table 5). The parametric analysis, however, did not reveal insula activation for the contrast FEAR.

Discussion

The present study investigated the neural correlates of fear and disgust using event-related fMRI in a parametric statistical design that considered each participant's individual evaluation of the stimuli with regard to feelings of disgust and fear.

Both fear and disgust ratings correlated with the activation of occipito-temporal regions,[1] prefrontal brain structures and the amygdala. This common activation pattern was observed in previous fMRI studies using categorical analyses, which contrast emotional conditions with a neutral condition (Phan et al., 2002; Stark et al., 2003, 2004; Bradley et al., 2003; Sabatinelli et al., 2005).

The amygdala was activated in response to both emotional categories, although its activation was stronger to disgust than to fear. Disgust-related amygdala activation has repeatedly been found (e.g. Britton et al., 2006; Schienle et al., 2006). Involvement of the amygdala in both fear and disgust has also been reported by Buchanan et al. (2004), who found that lesions including the amygdala reduced startle potentiation to disgust and fearful pictures. Furthermore, in a recent study by Fitzgerald et al.

[1] It is unlikely that the occipital activation pattern is due to the differences in viewing time (approximately 200 ms) between emotional and neutral pictures because every picture was modeled with the same duration of 4 s and activation patterns are similar to previous studies with constant presentation times (Stark et al., 2003, 2004).

Table 2
Significant activations for the explorative analysis of the parametric modulators DISGUST and FEAR and the contrasts DISGUST>FEAR and FEAR>DISGUST; in parentheses: proportion of brain structures within the cluster (only proportions ≥10% are displayed)

	H	*x*	*y*	*z*	Cs	Z_{max}
DISGUST						
Sup front gyrus, orbit part	R	18	30	−18	6	5.45 (sup front gyr, orbit part 100%)
Supramarg gyrus	R	63	−18	27	5	5.19 (supramarg gyr 80%, postcent gyr 20%)
Supramarg gyrus	L	−63	−24	30	21	6.10 (supramarg gyr 80%, postcent gyr 20%)
Inf temp gyrus	R	45	−60	−9	112	6.84 (inf temp gyr 70%, fusif gyr 17%, inf occip gyr 14%)
Inf temp gyrus	L	−45	−66	−6	280	7.82 (fusif gyr 31%, inf occip gyr 30%, inf temp gyr 20%, mid occip gyr 10%)
Mid occip gyrus	R	36	−87	12	28	5.91 (mid occip gyr 100%)
Mid occip gyrus	L	−36	−93	12	8	4.96 (mid occip gyr 100%)
Insula	R	39	3	−6	291	7.32 (insula 48%, hippoc 26%)
Insula	L	−39	0	−15	158	7.28 (insula 48%, hippoc 19%, sup temp gyr 14%, amyg 13%)
FEAR						
Inf front gyrus, triang part	R	54	33	0	32	5.73 (inf frontal gyr, triang part 94%)
Mid cingulate gyrus	L	−9	−48	33	71	5.18 (precuneus L 34%, post cing gyr 23%, precuneus R 17%, mid cing gyr 15%)
Fusiform gyrus	L	−42	−60	−18	71	5.97 (fusif gyr 72%, inf temp gyr 24%)
Mid temp gyrus	L	−51	−69	12	559	>10 (mid temp gyr 62%, mid occip gyr 32%)
Mid occip gyrus	R	45	−78	3	938	7.74 (mid temp gyr 53%, sup temp gyr 12%, mid occip gyr 6%)
Sup occip gyrus	L	−15	−96	18	14	5.16 (sup occip gyr 79%, cuneus 21%)
Sup occip gyrus	R	12	−99	18	52	6.87 (sup occip gyr 50%, cuneus 47%)
DISGUST>FEAR						
Fusiform gyrus	L	−27	−45	−18	67	5.84 (fusif gyr 79%, ling gyr 10%)
Fusiform gyrus	R	30	−51	−15	35	5.80 (fusif gyr 100%)
Inf temp gyrus	L	−45	−63	−6	11	5.88 (inf temp gyr 91%)
Mid occip gyrus	L	−33	−96	15	19	5.88 (mid occip gyr 100%)
Calcarine Fissure	R	21	−102	−6	20	5.63 (calcarine fiss 41%, inf occip gyr 29%, ling gyr 29%)
Insula	R	39	−3	3	28	6.01 (insula 100%)
Insula	L	−39	−6	6	18	5.54 (insula 94%)
FEAR>DISGUST						
Mid front gyrus	R	33	57	6	16	5.64 (mid front gyr 63%, sup front gyr 38%)
Inf front gyrus, orbit part	L	−48	42	−15	10	5.23 (inf front gyr, orbit part 100%)
Mid front gyrus, orbit part	L	−39	48	−3	59	5.53 (mid front gyr 58%, mid front gyr, orbit part 25%, sup front gyr 13%)
Mid front gyrus	R	42	27	39	38	5.47 (mid front gyr 89%, sup front gyr 11%)
Mid front gyrus	L	−42	27	39	15	5.25 (mid front gyr 100%)
Mid front gyrus	R	36	15	54	7	4.94 (mid front gyr 100%)
Cerebellum	R	42	−45	−30	23	5.51 (cerebellum 57%, fusif gyr 30%, inf temp gyr 13%)
Mid temp gyrus	R	63	−51	12	1227	7.75 (mid temp gyr 43%, ang part 27%, sup temp gyr 10%)
Precuneus	R	3	−60	42	1704	7.61 (precuneus R 35%, precuneus L 24%, cuneus 10%)
Mid occip gyrus	L	−45	−72	12	819	7.59 (mid temp gyr 38%, ang gyr 29%, mid occip gyr 16% inf pariet gyr 13%)
Sup occip gyrus	L	−12	−99	15	35	5.86 (sup occip gyr 79%, cuneus 21%)

The *p*-values were corrected for the total brain according to the random field theory. Coordinates *x*, *y*, and *z* are given in Montreal Neurological Institute space (H: hemisphere; Cs: cluster size).

(2006) with emotional facial expressions as stimuli, the amygdala responded to all of the five emotion categories including disgust and fear. These results fit well with the supposed role of the amygdala as a general evaluator of the reinforcement value of stimuli (Rolls, 1999; Zald, 2003). However some patient studies challenge this view. For example, Sprengelmeyer et al. (1999) described a patient with bilateral amygdala damage, whose ability to recognize and experience fear was specifically reduced while recognition and experience of disgust were left intact. Further research is needed to clarify the role of the amygdala in disgust processing.

Besides many similarities, the present study also revealed differences in the activation patterns between fear and disgust. Insula activation was associated with the disgust ratings, but not the fear ratings. Fear activated the middle temporal cortex and medial parietal structures (precuneus/posterior cingulate cortex), while disgust provoked an activation of the inferior temporal gyrus and (stronger than fear) the fusiform gyrus.

The correlation of insular activation with disgust ratings seems to contradict studies that found no insula activation under disgust stimulation (e.g. Schienle et al., 2006) or detected insula activation with fear-eliciting as well as disgust-inducing stimuli (e.g. Schäfer et al., 2005). One reason for this inconsistency could be that most of these studies did not include subjective evaluations of the stimulus material into their analyses. Yet, it should not be implicitly assumed that a certain stimulus will lead to homogenous responses within a group and equally that it can only trigger emotions of one category. For example, fear-eliciting

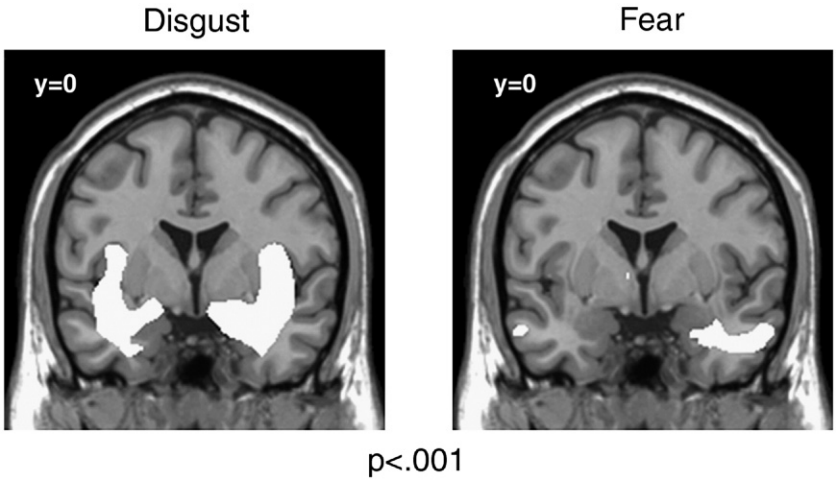

Fig. 2. Parametric analysis: activated voxels ($p<0.001$, uncorrected, cluster size ≥ 5) for the contrasts DISGUST and FEAR mapped onto the MNI brain template at $y=0$. Note that disgust-related brain activation includes all regions of interest bilaterally (insula, basal ganglia, and amygdala), while fear correlates only with activation of the right amygdala.

stimuli can also possess disgusting properties. This could explain insula activation to fear-inducing stimuli, given its frequently described specific role in disgust processing. Accordingly, the *categorical* analysis in the present study revealed significant insula activation under *both* fear and disgust conditions (see Table 5). The exclusive role of the insula, however, only became apparent in the *parametric* analysis. This role is supported by the fact that the primary gustatory and olfactory sensory cortices are located in the insula considering the close link between disgust and taste/smell. Additionally, lesions in the insula have been shown to lead to an impairment of disgust recognition (Calder et al., 2000; Adolphs et al., 2003) and a specific role for vomiting has also been reported (Augustine, 1996). Krolak-Salmon et al. (2003) recorded intracerebral event-related potentials (ERPs) to human facial emotional expressions using depth electrodes in patients with drug-refractory temporal lobe epilepsy. They found that the ventral anterior insula showed disgust-specific ERPs. Furthermore, a stimulation of this region led to unpleasant sensations in the throat in two patients. Although Krolak-Salmon et al. used faces as stimuli, some of their insula coordinates are close to the ones found in the present study.

A putative role of the insula in relation to interoception has also been discussed (for a review see Critchley, 2005). For example, Critchley et al. (2004) observed insula activation during an interoceptive task, in which the participants had to judge the timing of their own heartbeats. In the present study the rating procedure also required some kind of interoception. If disgust is accompanied by stronger visceral sensations (e. g. nausea) than fear, then the disgust-related insula activation could well be due to these physical reactions instead of disgust per se. An indication for the actual cause of the insula activation could be the localization of the activation within the insula. The insula coordinates of Critchley et al. (2004) and also Mathews et al. (2004), who also used a rating procedure, are more dorsal than those in the current study. The dorsal anterior insula might

Table 3
Significant activations for the region of interest analyses (ROI) of the parametric modulators DISGUST and FEAR and the contrasts DISGUST > FEAR (positive Z_{max}-values) and FEAR > DISGUST (negative Z_{max}-values) in the insula, the amygdala, and the basal ganglia

	DISGUST					FEAR					DISGUST < > FEAR				
	H	*x*	*y*	*z*	Cs	Z_{max}	*x*	*y*	*z*	Cs	Z_{max}	*x*	*y*	*z*	Cs	Z_{max}
Amygdala																
	R	33	0	−24	75	6.69	36	0	−27	35	4.41	30	3	−21	70	4.25
	L	−30	−3	−21	64	5.65						−24	−6	−15	56	3.91
Insula																
	R	39	3	−6	321	7.32						39	−3	3	226	6.01
	L	−39	0	−15	307	7.28						−39	−6	6	233	5.54
Basal ganglia																
	R	36	0	−3	96	5.34						36	0	−3	37	4.50
	R											15	24	−6	47	−3.74
	L	−18	3	−6	116	3.53										

The *p*-values were corrected for the ROI with $\alpha=0.05$. Coordinates *x*, *y*, and *z* are given in Montreal Neurological Institute space (H: hemisphere; Cs: cluster size).

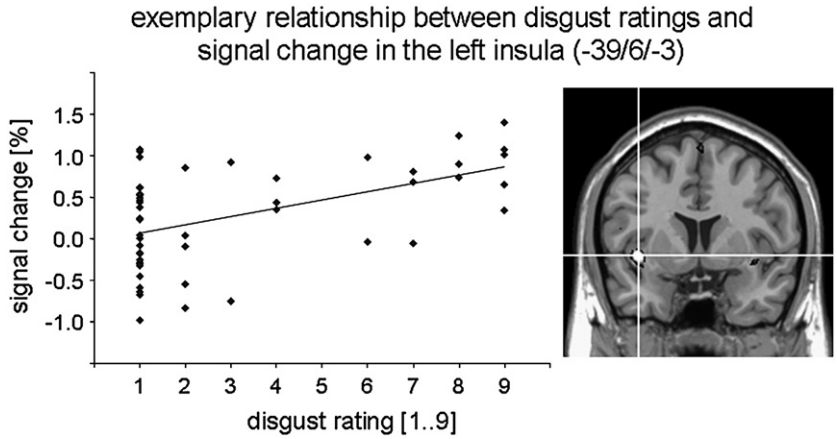

Fig. 3. Exemplary illustration of the parametric approach for a single participant. Signal change in the most sensitive voxel of the left insula in relation to the disgust ratings of the 50 pictures.

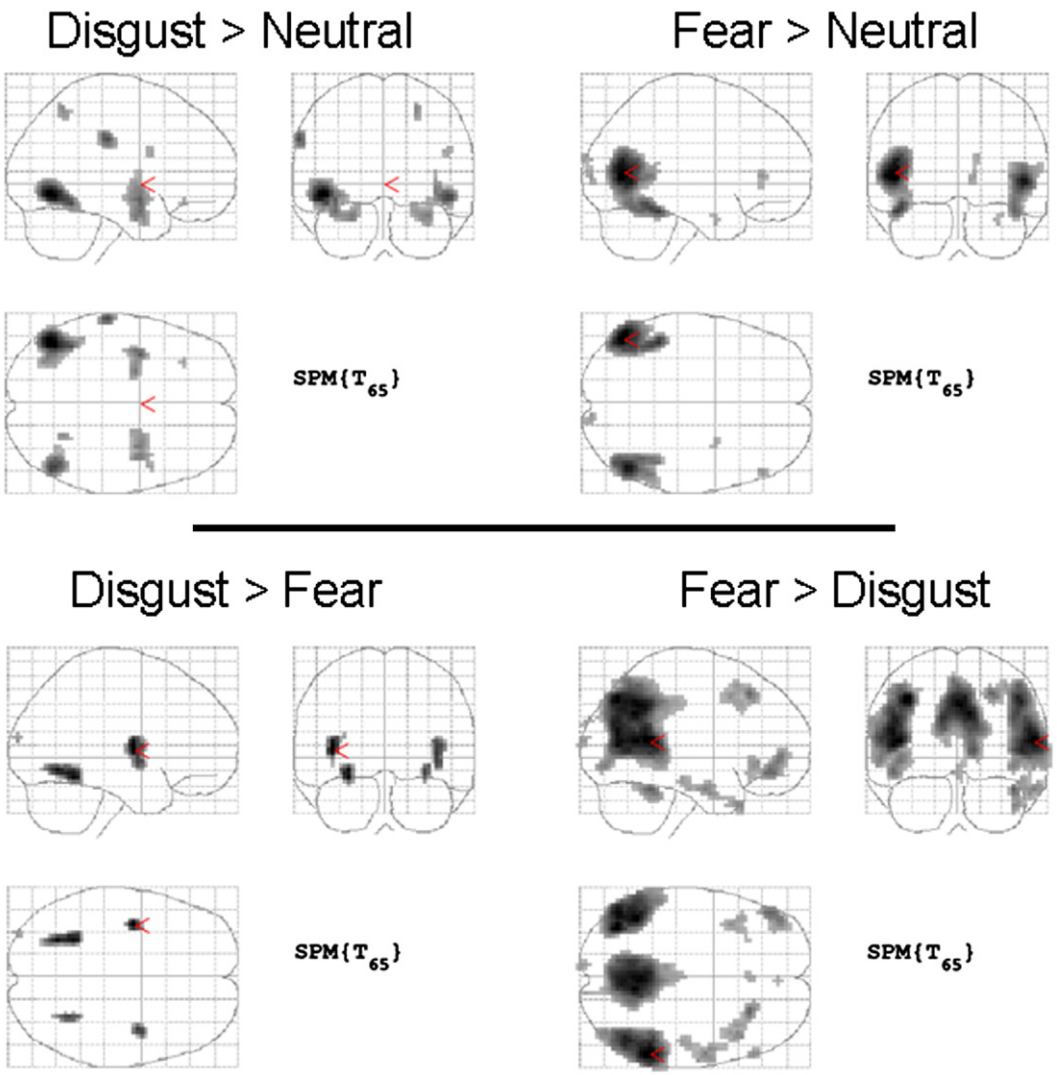

Fig. 4. Categorical analysis: activated voxels ($p<0.05$, whole brain corrected, cluster size ≥ 5) for the contrasts DISGUST>NEUTRAL, FEAR>NEUTRAL, DISGUST>FEAR, and FEAR>DISGUST in a random effect analysis.

Table 4
Significant activations for the explorative analysis of the categorical contrasts DISGUST>NEUTRAL, FEAR>NEUTRAL, DISGUST>FEAR, and FEAR>DISGUST; in parentheses: proportion of brain structures within the cluster (only proportions ≥10% are displayed)

	H	*x*	*y*	*z*	Cs	Z_{max}
DISGUST>NEUTRAL						
Inf front gyrus, orbit part	L	−30	33	−15	5	5.16 (inf front gyr, orbit part 80%, mid front gyr, 2orbit part 20%)
Inf front gyrus, operc part	R	48	9	24	12	5.21 (inf front gyr, operc part 92%)
Supramarginal gyrus	L	−63	−24	33	48	6.84 (supramarg gyr 70%, postcent gyr 30%)
Sup parietal gyrus	R	24	−57	57	20	5.74 (sup pariet gyr 74%, inf pariet gyr 26%)
Inf temp gyrus	R	48	−63	−9	122	7.02 (inf temp gyr 78%)
Inf temp gyrus	L	−45	−66	−9	323	>10 (inf temp gyr 30%, inf occip gyr 25%, fusif gyr 19%, mid temp gyr 16%)
Insula	L	−36	0	−12	130	6.53 (insula 43%, amyg 30%, hippoc 14%)
Amygdala	R	33	0	−24	143	6.05 (insula 41%, amyg 34%, sup temp pole 10%)
DISGUST>FEAR						
Fusiform gyrus	L	−27	−51	−15	91	6.54 (fusif gyr 68%, ling gyr 26%)
Fusiform gyrus	R	30	−54	−12	34	5.93 (fusif gyr 100%)
Mid occip gyrus	L	−33	−93	12	7	5.12 (mid occip gyr 100%)
Insula	R	39	−3	3	69	6.11 (insula 77%, roland operc 22%)
Insula	L	−39	−6	6	57	6.73 (insula 80%, roland operc 20%)
FEAR>NEUTRAL						
Inf front gyrus, triang part	R	54	36	6	19	5.59 (inf front gyr, triang part 100%)
Hippocampus	R	30	0	−30	8	5.07 (amyg 75%, hippoc 25%)
Mid temp gyrus	R	48	−66	3	526	7.82 (mid temp gyr 54%, inf temp gyr 19%, fusif gyr 11%)
Mid temp gyrus	L	−48	−69	9	774	>10 (mid temp gyr 43%, mid occip gyr 26%, inf temp gyr 10%)
Calcarine Fissure	R	9	−93	3	27	5.37 (calcarine fiss 50%, sup occip gyr 31%, cuneus 19%)
FEAR>DISGUST						
Med front gyrus, orbit part	R	3	48	−6	10	5.14 (med front gyr, orbit part R 70%, med front gyr, orbit part L 20%, sup front gyr, med part)
Inf front gyrus, orbit part	L	−48	42	−9	138	6.49 (inf front gyr, orbit part 33%, mid front gyr 32%, mid front)
Inf front gyrus, orbit part	R	57	30	−6	22	5.66 (inf front gyr, triang part 55%, inf front gyr, orbit part 45%)
Mid front gyrus	R	27	27	48	130	6.55 (mid front gyr 75%, sup front gyr 21%)
Med front gyrus, orbit part	L	0	27	−12	11	5.16 (med front gyr, orbit part R 55%, med front gyr, orbit part)
Mid front gyrus	L	−39	12	45	67	5.67 (mid front gyr 94%)
Mid temp gyrus	R	57	−6	−24	122	5.98 (mid temp gyr 60%, mid temp pole 23%, inf temp gyr)
Mid temp gyrus	R	57	−48	12	1496	>10 (mid temp gyr 44%, ang gyr 26%, sup temp gyr 10%)
Mid temp gyrus	L	−45	−57	12	1334	>10 (mid temp gyr 34%, ang gyr 27%, inf pariet gyr 15%)
Fusiform gyrus	R	42	−48	−24	47	6.62 (fusif gyr 40%, cerebellum 42%, inf temp gyr 17%)
Precuneus	R	3	−57	39	1781	>10 (precuneus R 32%, precuneus L 26%)
Sup occip gyrus	L	−9	−99	12	14	5.43 (sup occip gyr 54%, cuneus 38%)

The *p*-values were corrected for the total brain according to the random field theory. Coordinates *x*, *y*, and *z* are given in Montreal Neurological Institute space (H: hemisphere; Cs: cluster size).

therefore play a more general role for sensing one's own visceral bodily state (Jabbi et al., 2007) than the ventral anterior insula, which might be more disgust-related.

Brain activation in the middle/posterior cingulate cortex and precuneus was closely related to the ratings of fear. This region has often been found activated under emotional stimulation (Phan et al., 2002; Stark et al., 2004; Schäfer et al., 2005), especially in relation to episodic memory (Maddock et al., 2003). Another important function of the posterior cingulate is pain processing (Bromm, 2004; Ochsner et al., 2006). Although no pain stimuli were applied in the present study, many of the fear stimuli depicted attacks by animals and humans (e.g. violent scenes with knives or guns). A strong association of these stimuli with pain may have contributed to the observed posterior cingulate activation to fear stimuli.

Although the fear pictures were rated as more arousing than the disgust pictures, it is unlikely that the differences in fear- and disgust-related brain activation can be explained by this difference (see Table 1). Sabatinelli et al. (2005) showed that inferotemporal and amygdala activation to IAPS pictures was positively related to arousal. And yet, in the present study, it was the less arousing disgust stimuli that led to stronger activations in the amygdala and the inferior temporal gyrus, not the fear-eliciting pictures. Additionally, electrodermal reactions, as an indicator of arousal, did not differ significantly between the two emotional conditions.

A general limitation of subjective reports is, however, that they cannot be considered a direct readout of the experienced emotion. Despite the careful instruction of participants concerning the rating procedure, individual differences in the cognitive concepts of emotion can lead to a dissociation of the rating behaviour and the subjective experience. Yet, unlike most other studies, the present study required the participants to rate the emotional pictures immediately after the presentation in the

Table 5
Significant activations for the region of interest (ROI) of the categorical contrasts DISGUST>NEUTRAL, FEAR>NEUTRAL, DISGUST>FEAR (positive Z_{max}-values), and FEAR>DISGUST (negative Z_{max}-values) in the insula, the amygdala, and the basal ganglia

	DISGUST>NEUTRAL					FEAR>NEUTRAL					DISGUST<>FEAR				
H	*x*	*y*	*z*	Cs	Z_{max}	*x*	*y*	*z*	Cs	Z_{max}	*x*	*y*	*z*	Cs	Z_{max}
Amygdala															
R	33	0	−24	75	6.05	30	0	−27	66	4.94	24	−3	−18	66	4.82
L	−24	−3	−24	64	6.02	−21	−3	−27	51	5.05	−24	−6	−18	42	3.51
Insula															
R	39	0	−6	319	6.00	27	12	−21	96	4.29	39	−3	3	271	6.11
L	−36	0	−12	281	6.53	−36	0	−15	113	3.64	−39	−6	6	247	6.73
Basal ganglia															
R	36	0	−3	86	4.30						36	0	−3	53	4.74
R											15	6	15	203	−3.87
L	−33	0	−6	38	3.62						−6	18	−9	39	−3.51

The *p*-values were corrected for the ROI with $\alpha = 0.05$. Coordinates *x*, *y*, and *z* are given in Montreal Neurological Institute space (H: hemisphere; Cs: cluster size).

scanner. This aimed at avoiding memory and habituation effects. However, the influence of the rating procedure on the emotional reaction itself has to be considered. Generally, attention to emotion might either amplify or decrease emotion-related brain activation or it might not have any influence at all. Hutcherson et al. (2005) found in their fMRI study with emotional films that the rating procedure did not lead to decreased neural activations. Instead, it additionally activated emotion-related regions like the anterior cingulate cortex (ACC) and the insula. Lane et al. (1997) observed increased activation in the ACC, the medial prefrontal cortex, and the insula when participants attended to their subjective emotional responses to IAPS pictures compared with attention to spatial aspects of these pictures. In the study by Mathews et al. (2004), the participants' attention was directed either to emotional or to non-emotional aspects of fear-eliciting and neutral IAPS pictures. They found activation of the amygdala and the occipital cortex even under non-emotional distraction, concluding that the latter structures belong to an "obligatory" fear system. Nevertheless, the fear-related brain activation was stronger and included additional brain regions (e.g. insula, hippocampus, and cingulate cortex) in the emotional condition showing a clear modulation caused by attentional control. Although these results are not directly comparable to the present study, it can be assumed that the trial-by-trial rating of the pictures in the present study did – at the very least – not decrease the participants' emotional responses because it directed the participants' attention to the emotional aspects of the stimuli.

Conclusions

The debate on specific vs. common neural substrates for fear and disgust as a starting point, the present study investigated the hemodynamic brain correlates of these basic emotions by including participants' online evaluation of the stimuli into the analyses. Results show that the brain activations to fear and disgust overlapped in the extended occipital and prefrontal cortex, as well as in the amygdala. The fact that amygdala activation was stronger under disgust than under fear once again challenges the view of the amygdala as a selective fear processor. However, made possible by incorporating individual picture ratings, another important target region – the insular cortex – was found to be specifically related to the processing of the disgusting scenes. The brain systems processing fear and disgust were thus at least partially dissociable, showing that the common-component model of affective processing needs to be complemented by some degree of regional specialization.

Acknowledgments

This research was supported by a grant to R. Stark from the German Research Society (Az. STA 475/4-1).

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