Why are you looking like that? How the context influences evaluation and processing of human faces

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Perception and evaluation of facial expressions are known to be heavily modulated by emotional features of contextual information. Such contextual effects, however, might also be driven by non-emotional aspects of contextual information, an interaction of emotional and non-emotional factors, and by the observers' inherent traits. Therefore, we sought to assess whether contextual information about self-reference in addition to information about valence influences the evaluation and neural processing of neutral faces. Furthermore, we investigated whether social anxiety moderates these effects. In the present functional magnetic resonance imaging (fMRI) study, participants viewed neutral facial expressions preceded by a contextual sentence conveying either positive or negative evaluations about the participant or about somebody else. Contextual influences were reflected in rating and fMRI measures, with strong effects of self-reference on brain activity in the medial prefrontal cortex and right fusiform gyrus. Additionally, social anxiety strongly affected the response to faces conveying negative, self-related evaluations as revealed by the participants' rating patterns and brain activity in cortical midline structures and regions of interest in the left and right middle frontal gyrus. These results suggest that face perception and processing are highly individual processes influenced by emotional and non-emotional aspects of contextual information and further modulated by individual personality traits.

INTRODUCTION

In everyday life, faces appear within a situational context and are never seen completely isolated. In other words, face perception and evaluation are always influenced by contextual features. Indeed, several studies documented that emotional contexts change face perception (e.g. Kim *et al.*, 2004; Aviezer *et al.*, 2008; Boll *et al.*, 2011). However, the question remains in how far non-emotional aspects of contextual information work in concert with emotional features and whether these modulations of face perception depend on the observer's personality. To assess this question, we manipulated contextual information in terms of valence (emotional feature) and self-reference (non-emotional feature) independently in the present study. Furthermore, we investigated the impact of social anxiety as an inherent trait tightly connected to evaluation by peers.

Facial expressions often convey specific emotions that are recognized by others with high accuracy (Ekman and Rosenberg, 1997) and are known to engage brain regions that respond to emotional content such as the amygdala (Adolphs *et al.*, 1994; Said *et al.*, 2010) and the medial prefrontal cortex (mPFC; Vuilleumier and Pourtois, 2007; Heberlein *et al.*, 2008). Additionally, regions included in the basic circuit of face perception such as the fusiform gyrus and the superior/middle temporal gyrus (MTG; Haxby *et al.*, 2000; Said *et al.*, 2011) respond more strongly to emotional compared to neutral facial expressions (Sabatinelli *et al.*, 2011).

However, the interpretation of emotional facial expressions is not always clear-cut and is strongly influenced by the context such as previously encountered facial expressions (Russell and Fehr, 1987), previously heard stories (Carroll and Russell, 1996), simultaneously shown body postures (Aviezer *et al.*, 2008, 2011) or facial dynamics (Mühlberger *et al.*, 2011). Indeed, the perception of emotional faces seems to depend on an interaction of facial expression and contextual information (Righart and de Gelder, 2008a, 2008b; Herring *et al.*, 2011; Neta *et al.*, 2011), and associations between context and faces are routinely established (Barrett and Kensinger, 2010; Hayes *et al.*, 2010; Aviezer *et al.*, 2011). Using functional magnetic resonance imaging (fMRI), Kim *et al.* (2004) showed that brain responses to ambiguous emotional faces (surprise) were modified by context conditions. They found stronger amygdala activation for surprised faces embedded in negative compared to positive contexts, thus demonstrating context-dependent neural processing of the same emotional face. Taken together, a face's meaning and its perception are modulated by its context on the behavioral and neural level. Furthermore, this modulation, in turn, reflects back on the observer's opinion about the person 'behind' the face (Todorov and Uleman, 2002; Schiller *et al.*, 2009).

As a non-emotional contextual aspect, self-reference (i.e. whether the stimulus is related to the observer or not) may play a critical role for the processing of facial expressions. For instance, self-reference was shown to enhance memory and neurophysiological processing of emotional words (Fossati *et al.*, 2004; Herbert *et al.*, 2011). Brain imaging studies have shown that self-referential processing of emotional stimuli is associated with activity in medial prefrontal and cortical midline brain areas (Fossati *et al.*, 2003, 2004; Lemogne *et al.*, 2011; Philippi *et al.*, 2011), which might link sensory, self-referential and higher order processing of emotional stimuli (Northoff *et al.*, 2006).

In addition to situational contexts, individual traits such as social anxiety influence the perception and evaluation of social stimuli. Socially anxious individuals show an attentional, negative response bias and threat interpretation biases (Winton *et al.*, 1995; Beard and Amir, 2009; Wieser *et al.*, 2009a). They interpret neutral faces as more threatening and show increased HR responses than non-anxious participants (Yoon and Zinbarg, 2007, 2008; Wieser *et al.*, 2009b), and additionally have an increased capacity to detect threatening stimuli
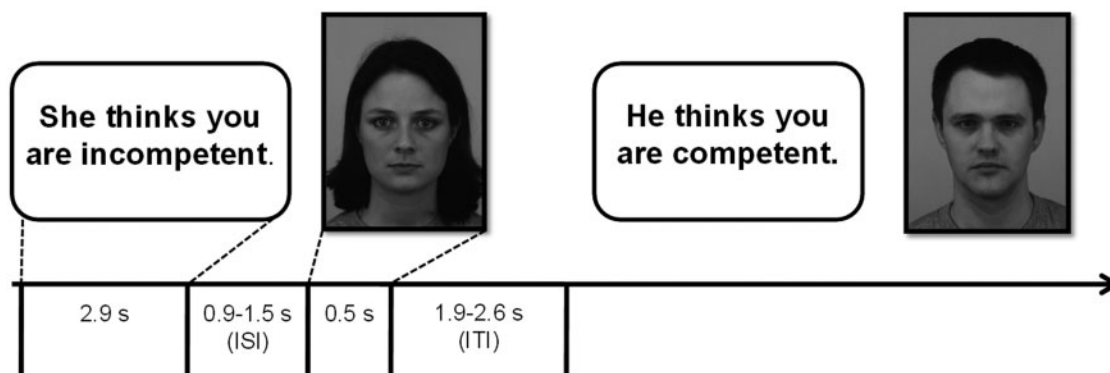
Fig. 1 Experimental paradigm (adapted and modified from Kim *et al.*, 2004). A fixation cross was shown during both, the interstimulus interval (ISI) and intertrial interval (ITI).

(Richards *et al.*, 2011). Although the effects of personality on the perception of social stimuli have been extensively studied in behavioral measures, functional neuroimaging studies often ignore these sources of variation in brain activity (cf. Calder *et al.*, 2011). However, recent studies point out that such personality traits have significant effects on the neural response to social stimuli (e.g. Manber-Ball *et al.*, 2012; Pardini and Phillips, 2010). Furthermore, neural activity in response to negative, self-related comments were shown to differ between individuals with pathological forms of social anxiety (i.e. social phobics) and a healthy control group (Blair *et al.*, 2008). Whether this change in neural activity is restricted to extreme values of social anxiety or whether it varies gradually with increasing levels of social anxiety is unknown and a major goal of the present study.

In addition to such a direct influence of individual traits on perception and processing of social stimuli, personality traits might also affect the interpretation of contextual information and thus indirectly modulate social perception. This indirect pathway could further enhance the influence of personality on social perception and behavior, especially in real world situations where context variables are not as controlled and sparse as in laboratory settings.

In the present fMRI study, we aimed to provide new insights into the fundamentals of social perception by investigating the effect of both, emotional (valence) and non-emotional (self-reference) context features on human face perception, while also considering interindividual variability (social anxiety). To this end, neutral facial expressions were cued with sentences producing different contextual situations (Figure 1). We used neutral facial expressions as social stimuli because of their ambiguous nature (Cooney *et al.*, 2006; Yoon and Zinbarg, 2008). The contextual information consisted of sentences conveying positive or negative evaluations about the participant or about somebody else, thus varying in valence and self-reference (cf. Blair *et al.* 2008).

In short, we addressed three research questions: (1) Is the evaluation and neural processing of neutral faces influenced by emotional contextual information (valence)? (2) Does contextual information about self-reference as a non-emotional feature lead to differential evaluation and neural processing of the face stimuli? (3) Are these processes modulated by the prominent fear of negative evaluation in socially anxious individuals?

We expected differential evaluation of the faces dependent on contextual condition and the observer's social anxiety level to be reflected in valence and arousal ratings. Regarding the neural activity, we focused primarily on the mPFC, which has been associated with self-referential processing (Northoff *et al.*, 2006), and basic face-processing areas (e.g. fusiform gyrus) that have been reported to respond more strongly to emotional compared to neutral faces

(Sabatinelli *et al.*, 2011). Moreover, brain activity in several areas in the prefrontal cortex including the middle frontal gyrus (MFG), inferior frontal gyrus (IFG) and superior frontal gyrus (SFG) was examined. These prefrontal areas are part of the frontoparietal control system that is activated during tasks requiring cognitive control (Vincent *et al.*, 2008; Yeo *et al.*, 2011). They have additionally been reported to respond more strongly to negative evaluation in social phobics (Blair *et al.*, 2008) or to emotional faces in general. The amygdala as a key node in emotion processing was also thoroughly investigated.

METHODS

Participants

Twenty-four female, right-handed (Edinburgh Handedness Inventory; Oldfield, 1971) students participated in this study ($M = 21.6$ years, s.d. $= 1.6$) in exchange for course credit. All participants reported normal or corrected-to-normal vision and no history of neurological or psychiatric disorders, and signed an informed consent form before participation. They completed the German version of the Brief Fear of Negative Evaluation (BFNE; Leary, 1983) with BFNE scores ranging from 18 to 51 ($M = 35.9$, s.d. $= 9.3$).

Stimulus material

The stimulus material consisted of neutral facial expressions of 40 individuals (20 women) of the KDEF inventory (Karolinska Directed Emotional Faces; Lundqvist *et al.*, 1998). Verbal stimuli derived from a pilot study consisted of five sentences, modified for the different context conditions (self-related/positive, self-related/negative, other-related/positive and other-related/negative; see Supplementary Data). Visual stimuli were presented via MRI-compatible goggles (VisuaStim; Magnetic Resonance Technologies, Northridge, CA, USA) controlled by Presentation 9.13 (Neurobehavioral Systems, Albany, CA, USA).

Paradigm

The experimental procedure was approved by the ethics committee of the medical faculty of the University of Würzburg. Participants passively viewed sentences and neutral facial expressions according to the paradigm established by Kim *et al.* (2004; Figure 1). Each sentence (self-related/positive, self-related/negative, other-related/positive and other-related/negative) was presented six times, three times with a male personal pronoun and three times with a female personal pronoun beginning the sentence.

Two distinct sets of pictures were used in the experiment, each comprising 10 male and 10 female faces. Each individual face was shown three times. One set was assigned to positive sentences, while

the other set was assigned to negative sentences. This assignment of picture sets to specific valences was counterbalanced across participants to ensure that differences in the BOLD response were not caused by intrinsic features of the faces (Kim *et al.*, 2004). Each session lasted about 20 min (including two short breaks) and consisted of 120 experimental trials and 30 zero trials (fixation cross).

After the scanning session, participants viewed the sentence and face stimuli again. They were asked to rate the faces in terms of valence (−4 = very negative to +4 = very positive) and arousal (1 = no emotional arousal at all to 9 = very strong emotional arousal).

fMRI data acquisition and analysis
fMRI scanner parameters
MR scanning was performed on a 1.5 Tesla whole-body tomograph (SIEMENS Avanto, Germany). Functional images were obtained using a T2*-weighted single-shot gradient echo-planar imaging (EPI) sequence (TR: 2500 ms, TE: 30 ms, 90° flip angle, FOV: 200 mm, matrix: 64 × 64, voxel size: $3.1 \times 3.1 \times 5$ mm^3). Each volume contained 25 axial slices parallel to the AC–PC plane (thickness 5 mm, 1 mm gap, interleaved order). Each session contained 510 functional images, of which the first seven were discarded to allow for T1 equilibration. Additionally, a high-resolution T1-weighted magnetization-prepared rapid gradient-echo imaging (MP-RAGE) 3D MRI sequence was obtained from each participant (TR: 2250 ms, TE: 3.93 ms, 98 flip angle, FOV: 256 mm, matrix: 256 × 256, voxel size: $1 \times 1 \times 1$ mm^3). Data were analyzed using Statistical Parametric Mapping software (SPM8; Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB 7.8 (The MathWorks, Inc.).

fMRI preprocessing
Functional images were slice time corrected and realigned. Then, the individual structural T1 image was coregistered to the mean functional image generated during realignment. Coregistered T1 images were then segmented using the 'New Segment' routine in SPM8. In the next step, EPI images were spatially normalized to MNI space (Montreal Neurological Institute) using the normalization parameters obtained from the segmentation procedure (voxel size $2 \times 2 \times 2$ mm^3) and smoothed with an 8-mm full-width-half-maximum (FWHM) Gaussian kernel.

fMRI first level
Each experimental condition (self-related/negative/face, other-related/negative/face, self-related/positive/face, other-related/positive/face, self-related/negative/sentence, other-related/negative/sentence, self-related/positive/sentence, other-related/positive/sentence and zero-trials) was modeled by convolving stick functions with the canonical hemodynamic response function (HRF), and parameter estimates pertaining to the amplitude of the HRF were calculated at each voxel, for each condition and each subject resulting in an individual contrast image for each condition. Realignment parameters for each session were included to account for residual movement-related variance. Parameter estimation was corrected for temporal autocorrelations using a first-order autoregressive model.

fMRI second level
Individual contrasts were analyzed in a random-effects model, focusing on comparisons between self *vs* other, and negative *vs* positive as well as simple effects of each condition against baseline. Interaction analyses were conducted by calculating the interaction contrast [(self/negative > other/negative) *vs* (self/positive > other/positive)].

ROI and whole-brain analysis
For a priori expected activations, ROI analyses were carried out in the amygdala, the fusiform gyrus, the superior/MTG and in the prefrontal cortex based on masks from WFU Pick Atlas (amygdala, Maldjian *et al.*, 2003) and coordinates of previous publications (MFG: Blair *et al.*, 2008; MFG, IFG, SFG, mPFC, fusiform gyrus, MTG: Sabatinelli *et al.*, 2011), respectively. In the latter case, spheres ($r = 5$ mm) were created centered on the reported peak voxels in the respective studies. Talairach coordinates were converted into MNI coordinates using the algorithm for nonlinear transformation as described in http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html. For whole-brain analyses, a threshold of $P < 0.001$, uncorrected for multiple comparisons and cluster size ≥ 10 voxels was applied; the threshold for ROI analyses was set to $P < 0.05$, familywise error corrected (FWE). Anatomical labeling was done by using the probabilistic stereotaxic cytoarchitectonic atlas implemented in the Anatomy Toolbox version 1.7 (Eickhoff *et al.*, 2005).

Correlation analysis
For correlation analysis, participants' BFNE scores were used as covariates in the second-level analysis. Additionally, β-values were extracted to compute ROI-wise correlations between social anxiety (as indexed by BFNE scores) and brain activity in self-related/negative, self-related/positive, other-related/negative and other-related/positive conditions.

RESULTS
Ratings
A 2×2 repeated measures ANOVA (within-subject factors self-reference and valence) showed a main effect of valence: neutral facial expressions in positive contexts were evaluated as more positive than in negative contexts ($M_{positive} = 0.20$, s.d.$_{positive} = 1.57$ *vs* $M_{negative} = -0.98$, s.d.$_{negative} = 1.43$; $F(1,23) = 29.56$, $P < 0.001$, $\eta_p^2 = 0.56$). A significant interaction of valence and self-reference showed that neutral faces in self-related positive contexts were rated as more positive, and neutral faces in self-related negative contexts as more negative than neutral faces in other-related positive or negative contexts, respectively, $F(1,23) = 17.58$, $P < 0.001$, $\eta_p^2 = 0.43$ (Table 1). In regard to arousal ratings, neutral faces in self-related contexts were perceived as more arousing than neutral faces in other-related contexts ($M_{self} = 3.93$, s.d.$_{self} = 2.04$ *vs* $M_{other} = 3.73$, s.d.$_{other} = 1.95$; $F(1,23) = 6.61$, $P = 0.017$, $\eta_p^2 = 0.22$). No other effect was significant (all F's < 1; for an analysis of the effects of the face's gender on valence and arousal ratings, see Supplementary Figure S1).

Furthermore, a correlation analysis revealed that fear of negative evaluation was associated with higher arousal ratings of faces in negative, self-related contexts compared to faces in negative, other-related contexts [correlation of BFNE scores and ($M_{self,negative} - M_{other,negative}$): $r = 0.431$, $P = 0.035$]. The correlation of valence ratings and BFNE

Table 1 Mean scores and s.d. in valence and arousal ratings for neutral facial expressions in the context conditions self-related/positive, self-related/negative, other-related/positive, other-related/negative

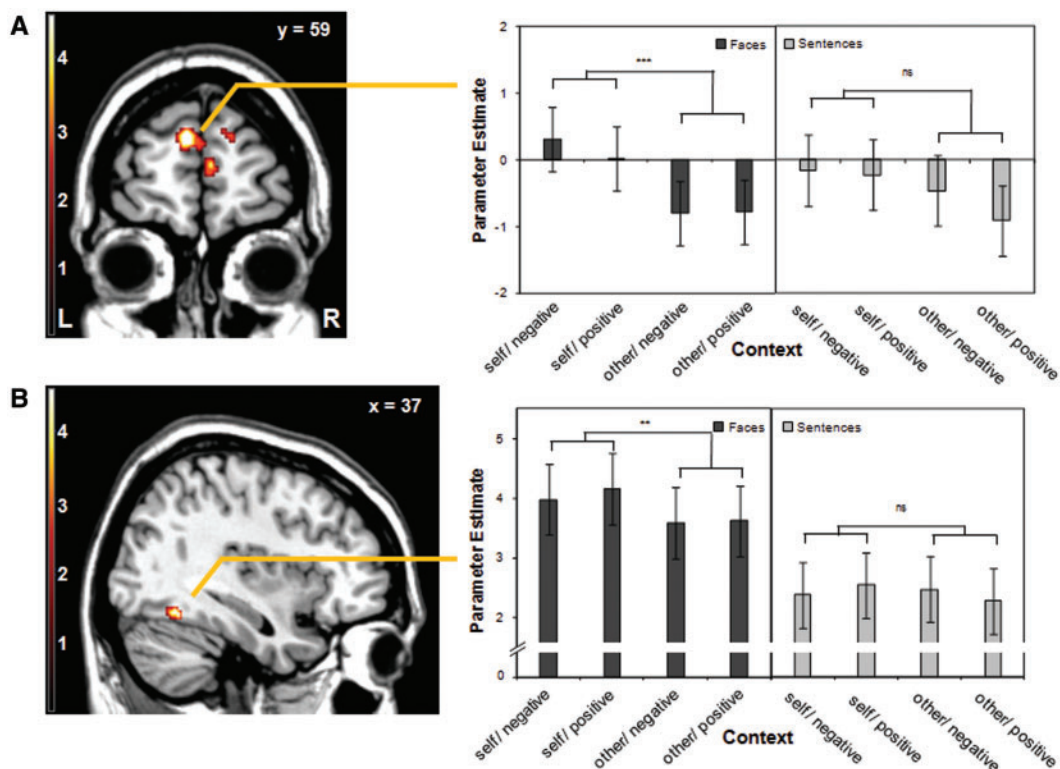|	Valence M (s.d.)	Arousal M (s.d.)
Self/positive	0.27 (0.76)	3.95 (1.46)
Self/negative	−1.14 (0.72)	3.92 (1.52)
Other/positive	0.14 (0.63)	3.77 (1.35)
Other/negative	−0.82 (0.55)	3.71 (1.42)

Fig. 2 Brain activity for the contrast *self-related vs other-related* (whole-brain analysis, $P < 0.005$, uncorrected, $k = 10$ contiguous voxels) and parameter estimates extracted from a sphere ($r = 5$ mm) centered on the respective peak voxel. (**A**) Increased activity in the medial prefrontal cortex (mPFC; $x = -6$, $y = 62$, $z = 22$). (**B**) Increased activity in the right fusiform gyrus ($x = 34$, $y = -58$, $z = -16$). Error bars represent 95% within-subject confidence intervals (CIs). ***$P < 0.001$, **$P < 0.005$.

scores did not reach significance but follows the same trend: The higher the participants' fear of negative evaluation the more negative were their ratings of faces in negative, self-related contexts compared to faces in negative, other-related contexts [correlation of BFNE scores and ($M_{\text{self,negative}} - M_{\text{other,negative}}$): $r = -0.318$, $P = 0.130$]. As expected, no such correlations were found for faces in positive contexts.

The impact of self-reference and valence on brain responses
Faces
Whole-brain analysis revealed an effect of self-reference: neutral faces in self-related contexts elicited stronger activity in the mPFC (Figure 2A and Table 2; $Z = 3.82$; $P < 0.001$, uncorrected; $x = -6$, $y = 62$, $z = 22$) and in the right fusiform gyrus (Figure 2B and Table 2; $Z = 3.43$; $P < 0.001$, uncorrected; $x = 34$, $y = -58$, $z = -16$) compared to neutral faces in other-related contexts. As shown in Figure 2A, a stronger decrease of activity in response to faces in other-related conditions was observed compared to baseline (i.e. default network) activity.[1] Both, the activation in the mPFC and in the right fusiform gyrus coincide with regions reported to show enhanced activity in response to emotional compared to neutral faces (Sabatinelli *et al.*, 2011), as ROI analysis revealed [mPFC: $Z = 2.77$; $P = 0.027$ (FWE corrected); $x = 2$, $y = 50$, $z = 12$; fusiform gyrus: $Z = 3.28$; $P = 0.007$ (FWE corrected); $x = 36$, $y = -56$, $z = -16$]. No other clusters of activation were elicited in regions of interest.

Regarding the influence of contextual valence, whole-brain analysis revealed an area in the right precentral gyrus (BA 6) as being more activated in response to faces in negative conditions than in positive

[1]The mPFC has been repeatedly associated with the default network (Bar, 2007; Bluhm et al., 2011), so that an activity decrease, as can be seen in this case in other-related conditions, does not implicate a general decrease in activity, but simply a decrease compared to the default activity during fixation.

Table 2 Significant activations for main effects and interactions in response to neutral faces in different contexts

Contrast	x	y	z	mm³	Z	Brain region
Self > other	−6	62	22	472	3.82	Superior medial PFC L (BA 9)
	2	36	12	944	3.80	Anterior Cingulate/ Superior medial PFC R
	10	10	70	96	3.47	Superior frontal gyrus R (BA 6)
	34	−58	−16	216	3.43	Fusiform gyrus R
Other > self	60	−16	48	512	4.03	Postcentral gyrus R (BA 1 and 2)
	−28	6	48	224	3.90	Middle frontal gyrus L (BA 6)
	40	−22	16	112	3.44	Insula R (BA 13)
Negative > positive	56	2	44	104	3.51	Precentral gyrus R (BA 6)
Positive > negative	−	−	−	−	−	−
Interaction self-reference × valence	−44	−8	−6	88	3.35	Insula L (BA 13)

All activations are effects observed in whole-brain analysis significant at $P < 0.001$, uncorrected, and a minimum of $k = 10$ contiguous voxels (80 mm³).
L = left, R = right hemisphere, PFC = prefrontal cortex. The cluster with the largest number of significant voxels within each region is reported. Coordinates x, y and z are given in MNI space.

conditions, while the contrast of positive *vs* negative showed no supra-threshold activity (Table 2).

Amygdala activity was not significantly increased in response to neutral faces in negative contexts compared to positive contexts. Instead, ROI analyses (thresholded at $P < 0.005$, uncorrected) revealed pronounced amygdala activity in both context conditions (negative context *vs* baseline and positive context *vs* baseline). In a more conservative analysis (FWE corrected), several voxels still showed significant activity in the respective contrasts [negative context: right amygdala, $Z = 3.55$; $P = 0.012$ (FWE corrected); $x = 18$, $y = -8$,

Table 3 Significant activations for main effects and interactions in response to sentences

Contrast	x	y	z	mm^3	Z	Brain region
Self > other	10	18	66	88	3.65	SMA R
Other > self	12	−24	24	144	3.46	Thalamus R
Negative > positive	−	−	−	−	−	−
Positive > negative	−38	−8	56	176	3.84	Precentral gyrus L (BA 6)
	46	8	34	328	3.76	Inferior frontal gyrus R (BA 44)
	16	−76	14	184	3.76	Calcarine gyrus R (BA 17)
	34	−6	−8	304	3.72	Claustrum R
	22	−84	−4	120	3.63	Lingual gyrus R
	32	−86	−8	152	3.54	Inferior occipital gyrus R
	60	4	38	88	3.40	Precentral gyrus R (BA 6)
Interaction	−18	−44	−42	184	4.01	Cerebellar tonsil L
self-reference	−24	38	48	328	3.95	Superior frontal gyrus L (BA 8)
× valence	10	−46	−42	120	3.77	Cerebellar tonsil R
	−30	−20	−14	368	3.67	Parahippocampal gyrus L
	32	−26	14	176	3.67	Insula R

All activations are effects observed in whole-brain analysis significant at $P < 0.001$, uncorrected, and a minimum of $k = 10$ contiguous voxels (80 mm^3).
L = left, R = right hemisphere. The cluster with the largest number of significant voxels within each region is reported. Coordinates x, y, and z are given in MNI space.

$z = −14$; left amygdala, $Z = 3.04$; $P = 0.049$ (FWE corrected); $x = −22$, $y = −8$, $z = −16$; positive context: right amygdala, $Z = 3.10$; $P = 0.037$ (FWE corrected); $x = 20$, $y = −6$, $z = −14$; left amygdala, $Z = 3.12$; $P = 0.038$ (FWE corrected); $x = −18$, $y = −6$, $z = −18$].

To investigate interaction effects of self-reference and valence, whole-brain and ROI analyses were computed. In PFC brain regions, the fusiform gyrus, the MTG and in the amygdala, no interactions of self-reference and valence were found. Indeed, only a small area in the left insula showed a supra-threshold interaction effect (Table 2; $Z = 3.35$; $P < 0.001$, uncorrected; $x = −44$, $y = −8$, $z = −6$). This area was especially activated in response to faces in other related, positive contexts.

Sentences

Sentences alone did not elicit differential activity in the mPFC, the fusiform gyrus, the amygdala or any other predefined ROI in any contrast nor in the self-reference × valence interaction.[2] Indeed, the contrasts targeting self-reference and the contrast negative *vs* positive indicate only very few, if any, regions of differential activity in these conditions (Table 3). However, positive sentences evoked stronger brain activity than negative sentences in several regions. Moreover, an interaction of self-reference and valence was found in a few areas with all of them being most strongly activated in other-related, positive conditions (Table 3).

Fear of negative evaluation

Using correlation analysis, we investigated whether activity in the prefrontal cortex in response to negative evaluation (neutral faces in self-related, negative contexts) was significantly related to the participant's fear of negative evaluation which was measured in BFNE scores. In a whole-brain analysis, several brain regions showed significant correlations between activity in the contrast self-related/negative *vs* other-related/negative and BFNE scores including the left mPFC and the precuneus, a cortical midline structure (Figure 3A and Table 4). A highly significant correlation was revealed in a region in the left middle frontal gyrus ($Z = 4.18$; $P < 0.001$ (uncorrected); $x = −30$, $y = 28$, $z = 40$) that corresponds roughly to the prefrontal cortex area

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[2]In this case, the lack of differential amygdala activity in response to sentences of different valence could not be explained by increased amygdala activity in both, positive and negative conditions as neither the contrast positive sentences *vs* baseline nor the contrast negative sentences *vs* baseline revealed any significant differences in amygdala activity.

described in Blair *et al.* (2008) where a significant modulation of the BOLD signal in response to negative evaluation was found in social phobia patients. Indeed, when we conducted a ROI analysis with a sphere ($r = 5$ mm) centered on the PFC coordinates as reported by Blair *et al.*, we found the whole area highly correlated with BFNE scores for the contrast self-related/negative *vs* other-related/negative [Figure 3B and C; peak voxel: $Z = 4.03$; $P = 0.002$ (FWE corrected); $x = −30$, $y = 32$, $z = 42$]. In the same contrast, fear of negative evaluation scores also correlated with activity in an area of the right middle frontal gyrus that has been reported to respond more strongly to emotional faces than to neutral faces [Sabatinelli *et al.*, 2011; $Z = 2.88$; $P = 0.022$ (FWE corrected); $x = 52$, $y = 16$, $z = 30$].

ROI-analyses targeting the amygdala showed no correlation between amygdala activity and BFNE scores. No correlations of brain activity and BFNE scores were found for neutral faces in positive contexts.

DISCUSSION

The present study investigated the influence of emotional and non-emotional context features on the evaluation and neural processing of human faces. Furthermore, we investigated how these processes are modulated by the observer's social anxiety. To this end, participants viewed neutral facial expressions cued with sentences conveying contextual information about valence and self-reference.

The influence of self-reference

The data of the present study indicate that neutral faces in self-related contexts are evaluated as more intense than neutral faces in other-related contexts. The most pronounced differences in neural processing were found in the mPFC and the fusiform gyrus.

Differences in medial prefrontal activity were found in ventral and dorsal parts of the mPFC (following the nomenclature of Northoff *et al.*, 2006). The ventral mPFC in particular is associated with processing of self-referential or self-relevant stimuli (Phan *et al.*, 2004; Mitchell *et al.*, 2005, 2006; Moran *et al.*, 2006). Generally, the mPFC is involved in many cognitive processes relating to emotional stimuli, including reappraisal, evaluation and explicit reasoning (Ochsner and Gross, 2005; Northoff *et al.*, 2006), memory (e.g. Takashima *et al.*, 2006), mentalizing about other people's mental states (Mitchell *et al.*, 2006; Jenkins and Mitchell, 2010), first impressions (Schiller *et al.*, 2009), reality monitoring (Buda *et al.*, 2011), predictions about the future and contextual associations (e.g. Bar, 2007). Moreover, this mPFC region has been shown to be consistently involved in the processing of emotional stimuli (Sabatinelli *et al.*, 2011). The increased mPFC activity in response to faces in self-related compared to other-related contexts could thus be attributed to various processes. Faces conveying self-related evaluations could have evoked in turn a more profound assessment by the participants. Stronger associations between contextual information and face identity might have been formed, facilitating the prediction of future behavior or the recollection of those faces. Our study design does not allow us to evaluate what precise processes underlie the changes in neural response in the mPFC. However, considering both, fMRI and behavioral data, it seems reasonable to assume that self-related contextual information leads the participants to assign more relevance to neutral faces compared to other-related contextual information.

Enhanced activity in the right fusiform gyrus in response to self-related as compared with other-related conditions further supports this finding. The fusiform gyrus is part of the ventral visual processing stream (also referred to as 'what' pathway) that is involved in object and form recognition (Grill-Spector and Malach, 2004; Martin, 2007) and thus 'makes sense' of visual stimuli. Moreover, the fusiform gyrus is part of the basic circuit for face perception (e.g. Kanwisher *et al.*,
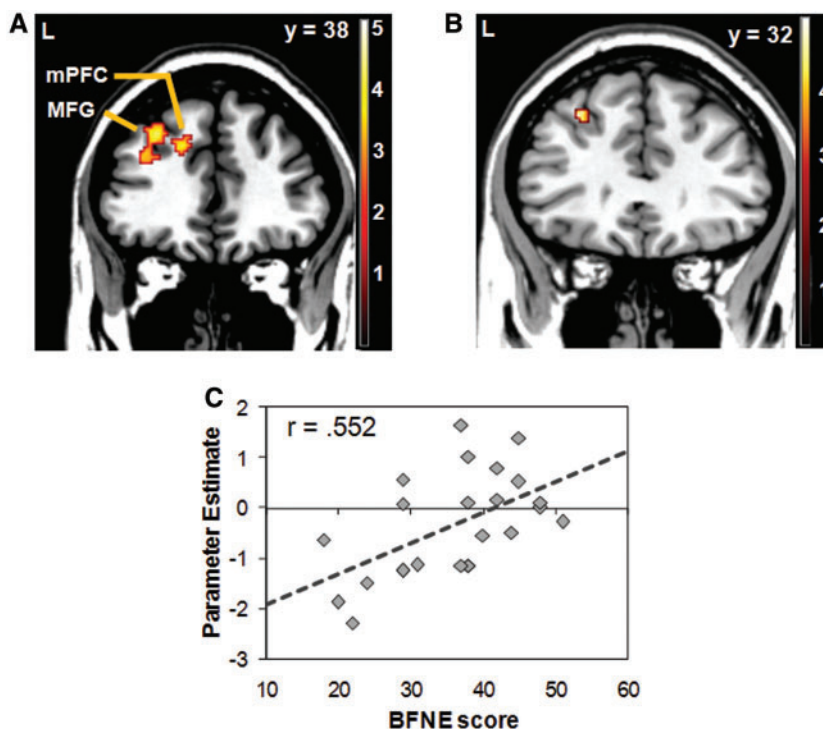
Fig. 3 (**A** and **B**) Correlation of the participants' Brief Fear of Negative Evaluation (BFNE) scores and brain activity in the contrast *self-related/negative vs other-related/negative.* (A) Whole-brain analysis ($P < 0.005$, uncorrected, $k = 10$ contiguous voxels) showing significant correlations with BFNE scores in the left medial prefrontal cortex (mPFC) and the left middle frontal gyrus (MFG). (B) ROI-analysis based on coordinates of Blair *et al.*, 2008, $P < 0.05$, FWE corrected, $k = 10$ contiguous voxels. The ROI lies within the left MFG activation that can also be seen in Figure 3A. (**C**) Correlation of the participants' BFNE scores with beta values extracted from the ROI based on coordinates of Blair *et al.* (2008); $r = 0.552$, $P = 0.005$. L = left.

Table 4 Significant correlations of BFNE scores and brain activity in the contrast neutral faces in self-related/negative *vs* other-related/negative contexts

x	y	z	mm³	Z	Brain region
−30	28	40	816	4.18	Middle frontal gyrus L
−16	38	32	88	3.42	Superior medial PFC/Superior PFC L
52	−2	46	576	3.95	Precentral gyrus R (BA 6)
28	54	12	112	3.60	Middle frontal gyrus R
0	−30	−42	200	3.93	Pons
−20	−2	12	104	3.66	Putamen L
−26	−56	−2	344	3.57	Lingual gyrus L
16	−78	42	96	3.48	Precuneus/Cuneus R (BA 7/19)

All activations are effects observed in whole-brain analysis significant at $P < 0.001$, uncorrected for multiple comparisons; $k > 10$ contiguous voxels (80 mm³).
L = left, R = right hemisphere, PFC = prefrontal cortex. The cluster with the largest number of significant voxels within each region is reported. Coordinates x, y, and z are given in MNI space.

1997; Haxby *et al.*, 2000). Besides its implication in fundamental object recognition, the fusiform gyrus is also involved in emotional processing showing consistently stronger activation to emotional stimuli compared to neutral stimuli (Lindquist *et al.*, in press; Sabatinelli *et al.*, 2011). Taken together, enhanced activity in the right fusiform gyrus in response to faces in self-related conditions compared to other-related conditions suggests that these faces are literally processed more profoundly than faces that are not self-related.

Both, the mPFC and the fusiform gyrus, were repeatedly reported to show stronger activation in response to emotional compared to neutral stimuli (Lindquist *et al.*, in press; Sabatinelli *et al.*, 2011). As only neutral facial expressions were used in this study, the enhanced activity in these regions in response to self-reference indicates that this non-emotional feature could have elevated the intrinsic value of the faces, thus increasing neural activity in regions assigning meaning to visual sensation.

Valence and the amygdala

Valence ratings clearly indicate that neutral facial expressions in positive contexts were perceived more positively than neutral facial expressions in negative contexts. Interestingly, the amygdala responded equally strong with above baseline activity for both, negative and positive contexts. At first sight, this finding seems counterintuitive because the amygdala was traditionally related to negative stimuli (e.g. Morris *et al.*, 1996). Challenging this traditional approach, the present data are in line with a growing body of literature showing amygdala activity in response to pleasant stimuli (Garavan *et al.*, 2001; Sergerie *et al.*, 2008; Klucken *et al.*, 2009), especially positive facial expressions (Breiter *et al.*, 1996; Yang *et al.*, 2002; Fitzgerald *et al.*, 2006). However, an alternative explanation cannot be ruled out, namely, that the amygdala merely responded to the perception of neutral faces independent of any differences in contextual valence. Findings about amygdala activity in response to neutral faces are ambiguous with some studies reporting amygdala activity in healthy subjects (e.g. Fitzgerald *et al.*, 2006) whereas others do not (e.g. Birbaumer *et al.*, 1998). Moreover, amygdala activity has been repeatedly reported in response to novelty or uncertainty (Lindquist *et al.*, in press; Wright *et al.*, 2003), attributes that both apply to the stimuli we used in this study. Since we did not include a truly neutral condition in the present study design,[3] we cannot pinpoint the exact reason for the observed pattern of results.

[3]Such a neutral condition was deliberately not implemented in the experimental design. In our opinion, no real neutral condition can be created when sentences are either self- or other-related. Sentences that might seem neutral when they are relating to someone else are usually perceived more negatively when they relate to oneself ('He thinks somebody's face is average looking' compared with 'He thinks your face is average looking'). If we had implemented such a condition, this effect would have made it very hard to correctly interpret our results.

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Taken together, the present findings suggest that in contrast to surprised faces as observed by Kim *et al.* (2004), amygdala reactivity in response to neutral faces seems not to be modulated by contextual changes in valence. This finding adds to the notion that the amygdala is implicated in the processing of both, positive and negative emotions, and works as a salience detector (Sander *et al.*, 2003). However, this interpretation has to be handled with care due to the lack of a truly neutral condition.

Social anxiety and negative evaluation

The present results suggest that personality traits such as social anxiety profoundly affect neural activity in response to trait-relevant information. The participants' social anxiety level (i.e. fear of negative evaluation) strongly influenced evaluation and neural processing of faces mediating negative self-related evaluations. This was particularly true for cortical midline structures such as the mPFC and the precuneus, as well as an area in the left middle frontal gyrus that was also identified by Blair *et al.* (2008) to be relevant in social phobia. Furthermore, an area in the right middle frontal gyrus that has been repeatedly associated with the processing of emotional compared to neutral faces (Sabatinelli *et al.*, 2011) showed the same activity pattern.

As mentioned above, enhanced activity in the mPFC in response to faces in self-related context conditions may be due to better mind perception, a more profound assessment of the evaluator by the participant, and stronger associations of contextual information and face identity. These explanations could also apply very well to the finding that enhanced activity in cortical midline structures in response to negative evaluation is highly correlated with the participant's social anxiety level. The more fear of negative evaluation an individual has, the more she might be inclined to assess the evaluator conveying this negative evaluation and the evaluator's mental state. The areas in the left and right middle frontal gyrus are also of particular interest because both have been implicated either directly in the processing of fear-relevant stimuli in social phobics (Blair *et al.*, 2008) or in the processing of emotional compared to neutral faces (Sabatinelli *et al.*, 2011). This differential modulation of the BOLD signal could be explained by the role of the middle frontal gyrus as part of the fronto-parietal control system in the detection of behaviorally relevant information. Enhanced activity in this area might indicate that more endogenous attention is assigned to stimuli conveying negative evaluation in participants with higher levels of social anxiety.

In general, the differences in neural responses dependent on social anxiety level indicate that stimuli conveying negative evaluations are perceived as more relevant by highly anxious individuals and thus more intensely attract their attention. This explanation is supported by our behavioral data that reveal a significant correlation of the participant's fear of negative evaluation and the arousal elicited by faces in negative, self-related contexts. This interpretation is also in line with studies reporting memory and attentional biases in individuals with pathological and subclinical levels of social anxiety, especially toward negative evaluation (for reviews, see Spurr and Stopa, 2002; Schultz and Heimberg, 2008), as well as recent EEG studies that revealed enhanced cortical processing of social threat stimuli (e.g. Wieser *et al.*, 2010, 2011).

In the present study, a significant amount of variance was accounted for by the influence of an individual trait. This systematic variance would usually be dismissed as noise or, with a small sample size, could even lead to systematic biases in neural measures, especially in between-subjects designs. Consequently, even when focusing on general mechanisms rather than individual responses, assessment of personality measures seems relevant to assure that changes in neuronal

activity are due to experimental manipulations and not personality-based confounds.

CONCLUSIONS

Taken together, the present results emphasize that the evaluation and processing of human faces are highly individual processes. Neural activity reflects the processing of target stimuli as well as context variables. Thereby, non-emotional context features have the potential to increase stimulus relevance working in concert with emotional features and individual traits. By neglecting the influence of context and personality in the research of perception, we possibly neglect an important part of what perception of everyday stimuli entails. Moreover, what holds true for the trait of (social) anxiety might also apply to other traits, such as extraversion, sensation seeking or self-concept. Personal experiences might shape reactions and interpretations as well as a person's current mood. It is important not to forget that in everyday life reactions to social stimuli do not strictly follow general rules—partly due to influences investigated in the present study.

SUPPLEMENTARY DATA

Supplementary Data are available at *SCAN* online.

Conflict of Interest

None declared.

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