

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

Katharina A. Schwarz,^{1,2} Matthias J. Wieser,¹ Antje B. M. Gerdes,^{1,3} Andreas Mühlberger,¹ and Paul Pauli¹

¹Department of Psychology, University of Würzburg, D-97070 Würzburg, Germany, ²Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, D-20246 Hamburg, Germany and ³Chair of Clinical and Biological Psychology, University of Mannheim, D-68131 Mannheim, Germany

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.

Keywords: facial expression; context; self-reference; social anxiety

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

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Correspondence should be addressed to Matthias J. Wieser, Department of Psychology, University of Würzburg, Marcusstrasse 9-11, D-97070 Würzburg, Germany. E-mail: wieser@psychologie.uni-wuerzburg.de

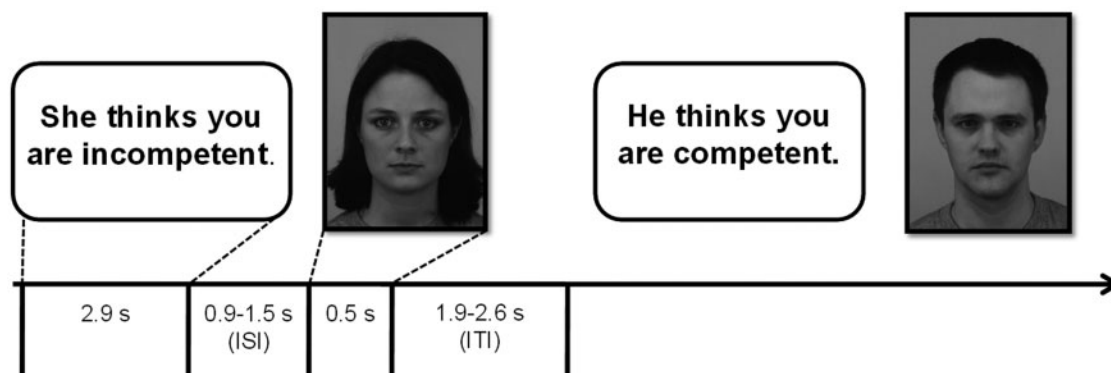


Fig. 1 Experimental paradigm (adapted and modified from Kim *et al.*, 2004). A fixation cross was shown during both, the interstimulus interval (ISI) and intertrial interval (ITI).

(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 ($-4 = \text{very negative}$ to $+4 = \text{very positive}$) and arousal ($1 = \text{no emotional arousal}$ at all to $9 = \text{very strong emotional arousal}$).

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: $3.1 \times 3.1 \times 5 \text{ mm}^3$). 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: $1 \times 1 \times 1 \text{ mm}^3$). 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 $2 \times 2 \times 2 \text{ mm}^3$) 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 ($r = 5 \text{ mm}$) 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 ($M_{\text{positive}} = 0.20$, $\text{s.d.}_{\text{positive}} = 1.57$ *vs* $M_{\text{negative}} = -0.98$, $\text{s.d.}_{\text{negative}} = 1.43$; $F(1,23) = 29.56$, $P < 0.001$, $\eta_p^2 = 0.56$). 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 ($M_{\text{self}} = 3.93$, $\text{s.d.}_{\text{self}} = 2.04$ *vs* $M_{\text{other}} = 3.73$, $\text{s.d.}_{\text{other}} = 1.95$; $F(1,23) = 6.61$, $P = 0.017$, $\eta_p^2 = 0.22$). 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 ($M_{\text{self,negative}} - M_{\text{other,negative}}$): $r = 0.431$, $P = 0.035$]. 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 <i>M</i> (s.d.)	Arousal <i>M</i> (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)

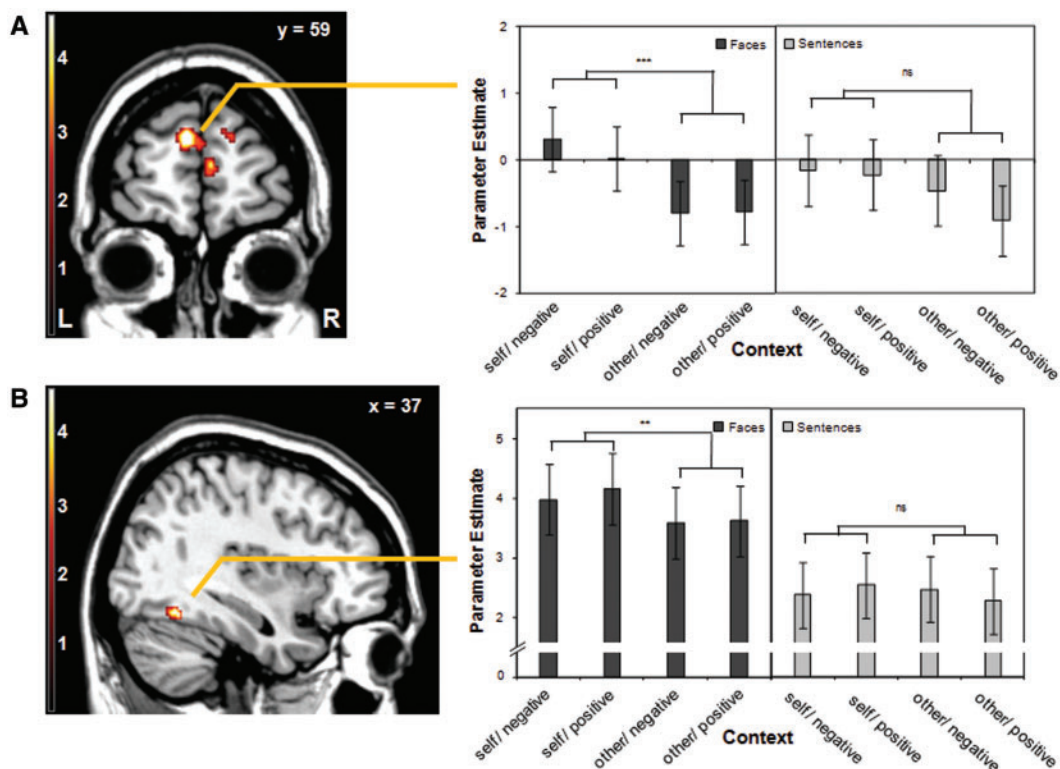


Fig. 2 Brain activity for the contrast *self-related vs other-related* (whole-brain analysis, $P < 0.005$, uncorrected, $k = 10$ contiguous voxels) and parameter estimates extracted from a sphere ($r = 5$ mm) centered on the respective peak voxel. (A) Increased activity in the medial prefrontal cortex (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 ($M_{self,negative} - M_{other,negative}$): $r = -0.318, P = 0.130$]. 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

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

Contrast	x	y	z	mm ³	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)
	56	2	44	104	3.51	Precentral gyrus R (BA 6)
Negative > positive	-	-	-	-	-	-
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 mm^3). 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); $x = 18, y = -8,$

¹The 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 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	Clastrum 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 \times 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

²In 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 ($r = 5 \text{ mm}$) 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.*,

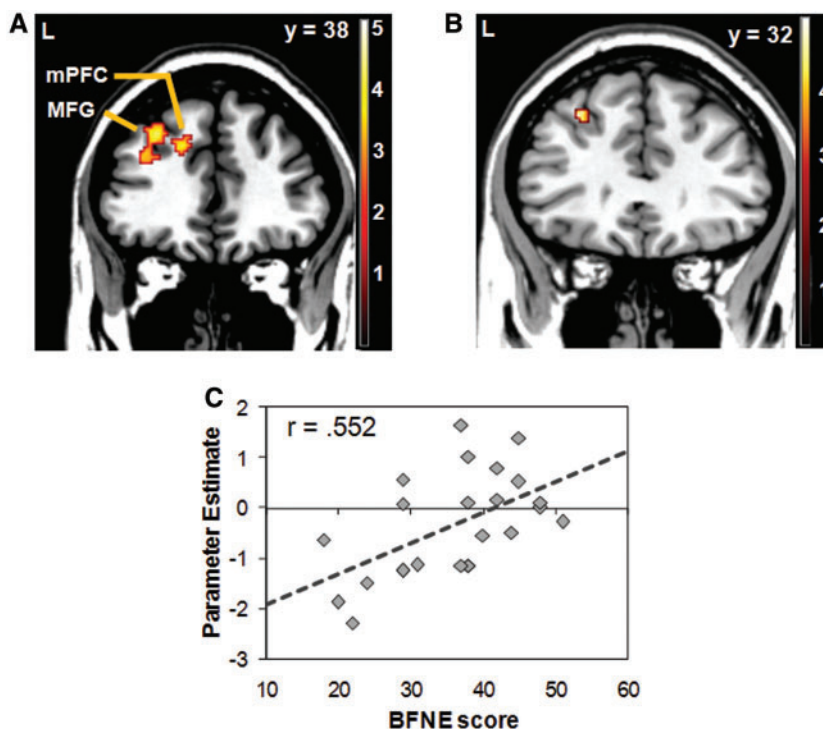


Fig. 3 (A and B) Correlation of the participants' Brief Fear of Negative Evaluation (BFNE) scores and brain activity in the contrast *self-related/negative vs other-related/negative*. (A) Whole-brain analysis ($P < 0.005$, uncorrected, $k = 10$ contiguous voxels) showing significant correlations with 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	mm ³	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.

³Such 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.

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 frontoparietal 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.

REFERENCES

- Adolphs, R., Tranel, D., Damasio, H., Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, 372, 669–72.
- Aviezer, H., Dudarev, V., Bentin, S., Hassin, R.R. (2011). The automaticity of emotional face-context integration. *Emotion*, 11, 1406–14.
- Aviezer, H., Hassin, R.R., Ryan, J., et al. (2008). Angry, disgusted, or afraid? Studies on the malleability of emotion perception. *Psychological Science*, 19, 724–32.
- Bar, M. (2007). The proactive brain: using analogies and associations to generate predictions. *Trends in Cognitive Sciences*, 11, 280–9.
- Barrett, L.F., Kensinger, E.A. (2010). Context is routinely encoded during emotion perception. *Psychological Science*, 21, 595–9.
- Beard, C., Amir, N. (2009). Interpretation in social anxiety: when meaning precedes ambiguity. *Cognitive Therapy and Research*, 33, 406–15.
- Birbaumer, N., Grodd, W., Diedrich, O., et al. (1998). fMRI reveals amygdala activation to human faces in social phobics. *NeuroReport*, 9, 1223–6.
- Blair, K., Geraci, M., Devido, J., et al. (2008). Neutral response to self- and other referential praise and criticism in generalized social phobia. *Archives of General Psychiatry*, 65, 1176–84.
- Bluhm, R.L., Clark, C.R., McFarlane, A.C., Moores, K.A., Shaw, M.E., Lanius, R.A. (2011). Default network connectivity during a working memory task. *Human Brain Mapping*, 32, 1029–35.
- Boll, S., Gamer, M., Kalisch, R., Büchel, C. (2011). Processing of facial expressions and their significance for the observer in subregions of the human amygdala. *NeuroImage*, 56, 299–306.
- Breiter, H.C., Etcoff, N.L., Whalen, P.J., et al. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron*, 17, 875–87.
- Buda, M., Fornito, A., Bergström, Z.M., Simons, J.S. (2011). A specific brain structural basis for individual differences in reality monitoring. *Journal of Neuroscience*, 31, 14308–13.
- Calder, A.J., Ewbank, M., Passamonti, L. (2011). Personality influences the neural responses to viewing facial expressions of emotion. *Philosophical Transactions of the Royal Society B Biological Sciences*, 366, 1684–701.
- Carroll, J.M., Russell, J.A. (1996). Do facial expressions signal specific emotions? Judging emotion from the face in context. *Journal of Personality & Social Psychology*, 70, 205–18.
- Cooney, R.E., Atlas, L.Y., Joormann, J., Eugene, F., Gotlib, I.H. (2006). Amygdala activation in the processing of neutral faces in social anxiety disorder: is neutral really neutral? *Psychiatry Research*, 148, 55–9.
- Eickhoff, S.B., Stephan, K.E., Mohlberg, H., et al. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, 25, 1325–35.
- Ekman, P., Rosenberg, E.L., editors (1997). *What the Face Reveals*. Oxford, England: Oxford University Press.

- Fitzgerald, D.A., Angstadt, M., Jelsone, L.M., Nathan, P.J., Phan, K.L. (2006). Beyond threat: amygdala reactivity across multiple expressions of facial affect. *NeuroImage*, 30, 1441–8.
- Fossati, P., Hevenor, S.J., Graham, S.J., et al. (2003). In search of the emotional self: an fMRI study using positive and negative emotional words. *American Journal of Psychiatry*, 160, 1938–45.
- Fossati, P., Hevenor, S.J., Lepage, M., et al. (2004). Distributed self in episodic memory: neural correlates of successful retrieval of self-encoded positive and negative personality traits. *NeuroImage*, 22, 1596–604.
- Garavan, H., Pendergrass, J.C., Ross, T.J., Stein, E.A., Risinger, R.C. (2001). Amygdala response to both positively and negatively valenced stimuli. *Neuroreport*, 12, 2779–83.
- Grill-Spector, K., Malach, R. (2004). The human visual cortex. *Annual Review of Neuroscience*, 27, 649–77.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I. (2000). The distributed neural system for face perception. *Trends in Cognitive Sciences*, 4, 223–33.
- Hayes, S.M., Baena, E., Truong, T.-K., Cabeza, R. (2010). Neural mechanisms of context effects on face recognition: automatic binding and context shift decrements. *Journal of Cognitive Neuroscience*, 22, 2541–54.
- Heberlein, A.S., Padon, A.A., Gillihan, S.J., Farah, M.J., Fellows, L.K. (2008). Ventromedial frontal lobe plays a critical role in facial emotion recognition. *Journal of Cognitive Neuroscience*, 20, 721–33.
- Herbert, C., Pauli, P., Herbert, B.M. (2011). Self-reference modulates the processing of emotional stimuli in the absence of explicit self-referential appraisal instructions. *SCAN*, 6, 653–61.
- Herring, D.R., Taylor, J.H., White, K.R., Crites, S.L. (2011). Electrophysiological responses to evaluative priming: the LPP is sensitive to incongruity. *Emotion*, 11, 794–806.
- Jenkins, A.C., Mitchell, J.P. (2010). Mentalizing under uncertainty: dissociated neural responses to ambiguous and unambiguous mental state inferences. *Cerebral Cortex*, 20, 404–10.
- Kanwisher, N., McDermott, J., Chun, M.M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17, 4302–11.
- Kim, H., Somerville, L.H., Johnstone, T., et al. (2004). Contextual modulation of amygdala responsivity to surprised faces. *Journal of Cognitive Neuroscience*, 16, 1730–45.
- Klucken, T., Schweckendiek, J., Merz, C.J., et al. (2009). Neural activations of the acquisition of conditioned sexual arousal: effects of contingency awareness and sex. *Journal of Sexual Medicine*, 6, 3071–85.
- Leary, M.R. (1983). A brief version of the fear of negative evaluation scale. *Personality and Social Psychology Bulletin*, 9, 371–5.
- Lemogne, C., Gorwood, P., Bergouignan, L., Péliolo, A., Lehericy, S., Fossati, P. (2011). Negative affectivity, self-referential processing and the cortical midline structures. *SCAN*, 6, 426–33.
- Lundqvist, D., Flykt, A., Öhman, A. (1998). *The Karolinska Directed Emotional Faces*. Stockholm: Karolinska Institutet.
- Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *NeuroImage*, 19, 1233–9.
- Manber-Ball, T., Sullivan, S., Flagan, T., et al. (2012). Selective effects of social anxiety, anxiety sensitivity, and negative affectivity on the neural bases of emotional face processing. *NeuroImage*, 59, 1879–87.
- Martin, A. (2007). The representations of object concepts in the brain. *Annual Review of Psychology*, 58, 25–45.
- Mitchell, J.P., Banaji, M.R., Macrae, C.N. (2005). The link between social cognition and self-referential thought in the medial prefrontal cortex. *Journal of Cognitive Neuroscience*, 17, 1306–15.
- Mitchell, J.P., Macrae, C.N., Banaji, M.R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron*, 50, 655–63.
- Moran, J.M., Macrae, C.N., Heatherton, T.F., Wyland, C.L., Kelley, W.M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience*, 18, 1586–94.
- Morris, J.S., Frith, C.D., Perrett, D.I., et al. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, 383, 812–5.
- Mühlberger, A., Wieser, M.J., Gerdes, A.B.M., Frey, M.C.M., Weyers, P., Pauli, P. (2011). Stop looking angry and smile, please: start and stop of the very same facial expression differentially activate threat- and reward-related brain networks. *SCAN*, 6, 321–9.
- Neta, M., Davis, F.C., Wahlen, P.J. (2011). Valence resolution of ambiguous facial expressions using an emotional oddball task. *Emotion*, 11, 1425–33.
- Northoff, G., Heinzel, A., de Greck, M., Birmpohl, F., Döbrowolny, H., Panksepp, J. (2006). Self-referential processing in our brain—a meta-analysis of imaging studies on the self. *NeuroImage*, 31, 440–57.
- Ochsner, K.N., Gross, J.J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences*, 9, 242–9.
- Oldfield, R.C. (1971). The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia*, 9, 97–113.
- Pardini, D.A., Phillips, M. (2010). Neural responses to emotional and neutral facial expressions in chronically violent men. *Journal of Psychiatry & Neuroscience*, 35, 390–8.
- Phan, K.L., Taylor, S.F., Welsh, R.C., Ho, S.H., Britton, J.C., Liberzon, I. (2004). Neural correlates of individual ratings of emotional salience: a trial-related fMRI study. *NeuroImage*, 21, 768–80.
- Philippi, C.L., Duff, M.C., Denburg, N.L., Tranel, D., Rudrauf, D. (2012). Medial pFC damage abolishes the self-reference effect. *Journal of Cognitive Neuroscience*, 24, 475–81.
- Richards, H.J., Hadwin, J.A., Benson, V., Wenger, M.J., Donnelly, N. (2011). The influence of anxiety on processing capacity for threat detection. *Psychonomic Bulletin & Review*, 18, 883–9.
- Righart, R., de Gelder, B. (2008a). Recognition of facial expressions is influenced by emotional scene gist. *Cognitive, Affective, & Behavioral Neuroscience*, 8, 264–72.
- Righart, R., de Gelder, B. (2008b). Rapid influence of emotional scenes on encoding of facial expressions: an ERP study. *SCAN*, 3, 270–8.
- Russell, J.A., Fehr, B. (1987). Relativity in the perception of emotion in facial expressions. *Journal of Experimental Psychology: General*, 116, 223–37.
- Sabatinelli, D., Fortune, E.E., Li, Q., Siddiqui, A., et al. (2011). Emotional perception: meta-analysis of face and natural scene processing. *NeuroImage*, 54, 2524–33.
- Said, C.P., Dotsch, R., Todorov, A. (2010). The amygdala and FFA track both social and non-social face dimensions. *Neuropsychologia*, 48, 3596–605.
- Said, C.P., Haxby, J.V., Todorov, A. (2011). Brain systems for assessing the affective value of faces. *Philosophical Transactions of the Royal Society B Biological Sciences*, 366, 1660–70.
- Sander, D., Grafman, J., Zalla, T. (2003). The human amygdala: an evolved system for relevance detection. *Reviews in the Neurosciences*, 14, 303–16.
- Schiller, D., Freeman, J.B., Mitchell, J.P., Uleman, J.S., Phelps, E.A. (2009). A neural mechanism of first impressions. *Nature Neuroscience*, 12, 508–14.
- Schultz, L.T., Heimberg, R.G. (2008). Attentional focus in social anxiety disorder: potential for interactive processes. *Clinical Psychology Review*, 28, 1206–21.
- Sergerie, K., Chochol, C., Armony, J.L. (2008). The role of the amygdala in emotional processing: a quantitative meta-analysis of functional neuroimaging studies. *Neuroscience and Biobehavioral Reviews*, 32, 811–30.
- Spurr, J.M., Stopa, L. (2002). Self-focused attention in social phobia and social anxiety. *Clinical Psychology Review*, 22, 947–75.
- Takashima, A., Petersson, K.M., Rutters, F., et al. (2006). Declarative memory consolidation in humans: a prospective functional magnetic resonance imaging study. *PNAS*, 103, 756–61.
- Todorov, A., Uleman, J.S. (2002). Spontaneous trait inferences are bound to actors' faces: evidence from a false recognition paradigm. *Journal of Personality and Social Psychology*, 83, 1051–65.
- Vincent, J.L., Kahn, I., Snyder, A.Z., Raichle, M.E., Buckner, R.L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, 100, 3328–42.
- Vuilleumier, P., Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. *Neuropsychologia*, 45, 174–94.
- Wieser, M.J., Pauli, P., Alpers, G.W., Mühlberger, A. (2009a). Is eye to eye contact really threatening and avoided in social anxiety? An eye-tracking and psychophysiology study. *Journal of Anxiety Disorders*, 23, 93–103.
- Wieser, M.J., Pauli, P., Weyers, P., Alpers, G.W., Mühlberger, A. (2009b). Fear of negative evaluation and the hypervigilance-avoidance hypothesis: an eye-tracking study. *Journal of Neural Transmission*, 116, 717–23.
- Wieser, M.J., McTeague, L.M., Keil, A. (2011). Sustained preferential processing of social threat cues: bias without competition? *Journal of Cognitive Neuroscience*, 23, 1973–86.
- Wieser, M.J., Pauli, P., Reicherts, P., Mühlberger, A. (2010). Don't look at me in anger! Enhanced processing of angry faces in anticipation of public speaking. *Psychophysiology*, 47, 271–80.
- Winton, E.C., Clark, D.M., Edelmann, R.J. (1995). Social anxiety, fear of negative evaluation and the detection of negative emotion in others. *Behaviour Research and Therapy*, 33, 193–6.
- Wright, C.I., Martis, B., Schwartz, C.E., et al. (2003). Novelty response and differential effects of order in the amygdala, substantia innominata, and inferior temporal cortex. *NeuroImage*, 18, 660–9.
- Yang, T.T., Menon, V., Eliez, S., et al. (2002). Amygdala activation associated with positive and negative facial expressions. *NeuroReport*, 13, 1737–41.
- Yeo, B.T.T., Krienen, F.M., Sepulcre, J., et al. (2011). The organization of the human cerebral cortex estimated by functional connectivity. *Journal of Neurophysiology*, 106, 1125–65.
- Yoon, K.L., Zinbarg, R.E. (2007). Threat is in the eye of the beholder: social anxiety and the interpretation of ambiguous facial expressions. *Behaviour Research and Therapy*, 45, 839–47.
- Yoon, K.L., Zinbarg, R.E. (2008). Interpreting neutral faces as threatening is a default mode for socially anxious individuals. *Journal of Abnormal Psychology*, 117, 680–5.