

## When vocal processing gets emotional: On the role of social orientation in relevance detection by the human amygdala

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Received 20 July 2007; revised 14 November 2007; accepted 13 January 2008

Available online 26 January 2008

Previous work on vocal emotional processing provided little evidence for involvement of emotional processing areas such as the amygdala or the orbitofrontal cortex (OFC). Here, we sought to specify whether involvement of these areas depends on how relevant vocal expressions are for the individual. To this end, we assessed participants' social orientation — a measure of the interest and concern for other individuals and hence the relevance of social signals. We then presented task-irrelevant syllable sequences that contained rare changes in tone of voice that could be emotional or neutral. Processing differences between emotional and neutral vocal change in the right amygdala and the bilateral OFC were significantly correlated with the social orientation measure. Specifically, higher social orientation scores were associated with enhanced amygdala and OFC activity to emotional as compared to neutral change. Given the presumed role of the amygdala in the detection of emotionally relevant information, our results suggest that social orientation enhances this detection process and the activation of emotional representations mediated by the OFC. Moreover, social orientation may predict listener responses to vocal emotional cues and explain interindividual variability in vocal emotional processing.

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**Keywords:** Affective; Prosody; Mismatch negativity; Sex differences; Collectivism; Deviance detection

### Introduction

Sensitivity to the emotional state of others is a prerequisite for successful navigation within social groups (Darwin, 1872; Baron-

Cohen, 1992). It allows individuals to predict the behavior of interaction partners and thus to flexibly employ strategies that increase the probability of obtaining the desired interaction outcome (e.g., marriage, business contract). Among the different nonverbal channels that humans use for emotional communication, the vocal channel is especially important because it can carry over large distances and is independent of sight. Moreover, it can be used to communicate emotions in a non-linguistic context in form of emotionally charged exclamations, such as laughs or sighs, or as prosody in the context of speech. The brain structures that support the processing of emotional exclamations or prosody have been investigated in a number of patient and neuroimaging studies (for a review see Schirmer and Kotz, 2006). Not surprisingly, this research implicates areas involved in various aspects of cognition ranging from perception to semantic memory and language. Specifically, vocal processing seems to be mediated by a pathway that extends from primary and secondary auditory cortex to regions along the bilateral superior temporal sulcus (STS). The STS has been proposed to include voice selective areas (Belin et al., 2004) that are specifically engaged in the processing of vocal as compared to non-vocal, environmental sounds (e.g., tool sounds). Interestingly, activity in these regions appears to be enhanced if vocal sounds are emotional as demonstrated by studies that compared emotional and neutral tone of voice (e.g., Grandjean et al., 2005; Kotz et al., 2003) or that correlated emotional intensity with fMRI signal changes (e.g., Ethofer et al., 2006; Wiethoff et al., 2008). This suggests that the STS is involved in the analysis of vocal emotional information. Moreover, in line with primate work demonstrating projections from this region to the frontal lobes (Petrides and Pandya, 1988), it has been proposed that the results of vocal processing at the level of the STS serve as input to higher order cognitive processes mediated by the frontal lobes (Schirmer and Kotz, 2006). Accordingly, there is evidence that vocal emotional judgments activate the right inferior frontal gyrus (IFG) relative to acoustic or linguistic judgments (Buchanan et al., 2000; Gandour et al., 2003; Wildgruber et al., 2002; Wildgruber et al.,

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

2004; Wildgruber et al., 2005; but see Mitchell et al., 2003). As right IFG involvement seems to depend on listeners actively evaluating the perceived stimuli on an emotional dimension, one may conclude that the right IFG plays a special role in the conscious evaluation of vocal emotional exclamations or prosody. Increased activity in the left IFG has been observed in response to emotional words spoken with incongruous as compared to congruous emotional prosody, suggesting that this area is implicated in the integration of verbal and vocal cues (Schirmer et al., 2004; Mitchell, 2006). In addition to these more cognitive processes, emotional vocalizations have also been shown to activate structures associated with the elicitation of emotional or feeling states. For example, emotional vocalizations were found to elicit activity in the bilateral orbitofrontal cortex (OFC; Wildgruber et al., 2002; Wildgruber et al., 2004; Sander et al., 2005), a structure which presumably represents the reinforcement value of a given stimulus (i.e., its rewarding or punishing nature) and mediates emotional responses via connections to the amygdala (Kringelbach and Rolls, 2004). In line with this, some investigations on the processing of emotional exclamations (Fecteau et al., 2007; Phillips et al., 1998; Sander and Scheich, 2001; but see Meyer et al., 2005) and emotional prosody (Sander et al., 2005; but see Ethofer et al., 2006; Kotz et al., 2003; Mitchell et al., 2003; Morris et al., 1999; Wiethoff et al., 2008) also reported amygdala activation. However, these reports frequently relied on a more liberal statistical threshold and are, particularly in the case of prosody, relatively sparse.

The minimal support for the involvement of OFC and amygdala in vocal emotional processing stands in contrast to the more consistent evidence that implicates these areas in the processing of other types of emotional stimuli. For example, emotional pictures (e.g., Britton et al., 2006) odors (e.g., Gottfried et al., 2003) or facial expressions (e.g., Vuilleumier et al., 2001; Vuilleumier et al., 2004; for a review see Adolphs, 2002) reliably activate the amygdala and the OFC. One possible explanation for the discrepancy between this work and the research on vocal processing may be that the vocal material used in the latter studies is simply less emotionally provoking and hence less likely to recruit emotion centers in the brain. In line with this argument, emotional exclamations (e.g., laughing, crying) – which are presumed to be more emotionally charged than the prosodic expressions that accompany speech – are more likely to activate the amygdala (Fecteau et al., 2007; Phillips et al., 1998; Sander and Scheich, 2001). Additionally, interindividual differences in the emotional response to prosodic signals may contribute to inconsistencies in the reported activations. If not taken into account, such interindividual differences may obscure amygdala and OFC contribution to stimulus processing especially when the emotionality of a given stimulus is relatively low.

Support for a role of interindividual differences in vocal and more specifically in prosodic emotional processing comes from a number of studies. For example, as for other channels of communication (e.g., Hamspon et al., 2006), women have been shown to recognize emotional-prosodic cues faster and more accurately than men (Hall, 1978; Dromey et al., 2005; Schirmer and Kotz, 2003; but see Fecteau et al., 2005). Furthermore, women are more likely to differentiate between emotional and neutral prosody when these prosodic stimuli are unattended (Schirmer et al., 2005). Women are also more likely to integrate unattended prosodic cues into language processing as demonstrated by facilitated processing of words that correspond in valence to the speaker's emotional prosody (e.g., "success" spoken with a happy tone; Schirmer and Kotz, 2003; Schirmer et al., 2004; but see Kotz and Paulmann, 2007). These

findings have been interpreted in light of women's role in the caring for offspring and their presumably greater affiliative tendencies (Babchuk et al., 1985; Hamspon et al., 2006; Taylor et al., 2000). Accordingly, it has been proposed that the emotional quality of vocal expressions is more relevant to women than to men and hence women tend to be more proficient in using vocal cues.

Additionally, interindividual differences in emotion recognition have been revealed by cross-cultural comparisons (e.g., Yuki, Maddux, Masuda, 2007). With respect to the present study, work by Kitayama and colleagues (Kitayama and Ishii, 2002; Ishii et al., 2003) on emotional-prosodic processing is of importance. The authors presented positive and negative words spoken with either a congruous or an incongruous emotional prosody to Asian and Western listeners. In different tasks, participants were asked to judge verbal content while ignoring prosody or to judge prosody while ignoring verbal content. Asian listeners from Japan and the Philippines had greater difficulty ignoring prosody, whereas the reversed pattern was observed for North American listeners. The authors concluded from these results that Asian and Western listeners differ in the sensitivity to vocal emotional signals. Moreover, the authors speculated that because Asian listeners come from a collectivistic cultural background, which places greater emphasis on an individual's ability to accurately interpret subtle emotional signals, these signals are of greater relevance. As a consequence, listeners with a collectivistic cultural background may process vocal emotional information in a more automatized fashion than listeners with an individualistic background.

These processing differences and the differences that have been identified between male and female listeners are interesting in the context of equivocal neuroimaging findings concerning the role of amygdala and OFC during vocal emotional processing. Based on the above evidence it seems that in order to study the role of these structures it might be useful to consider the individual and to identify variables that drive his or her emotional response to vocal signals. Given that current proposals to explain gender and cultural differences in vocal emotional processing evoke the relevance of vocal expressions for the individual, we speculated that a personality trait that captures this relevance would be a variable of interest. From among the dimensions that psychologists use to characterize an individual's personality (e.g., extraversion, neuroticism), we identified "social orientation" as being most clearly linked to the relevance of social signals such as vocal expressions. Social orientation reflects an individual's interest in social exchange and the extent to which he or she cares about other individuals (Andsager et al., 2006; Soares et al., 2005). Psychologists assess social orientation by means of questionnaires which may include true/false questions such as "I feel responsible for individuals beyond my immediate family" or "If I see a person cry I feel the need to comfort him or her". Generally, women score higher than men on measures of social orientation (Fahrenberg et al., 1994). Furthermore, as collectivism emphasizes the importance of the group over the individual (Hofstede, 1980), individuals from a collectivistic culture typically score higher on measures of social orientation than do individuals from an individualistic culture (Hofstede, 1980; Conway et al., 2005). Taken together this evidence supports the idea that interindividual differences in social orientation may underlie previously observed gender and cultural differences in vocal emotional processing. Thus, one may hypothesize that social orientation modulates the relevance of vocal signals and thereby influences the processing of and emotional response to these signals.

In the present fMRI study, we sought to determine the relationship between social orientation and vocal emotional processing. Specifically, we used an auditory oddball paradigm which has been tested in a prior event-related potential (ERP) study and shown to be sensitive to interindividual differences (Schirmer et al., 2005). In this paradigm, participants watch a silent movie with subtitles while an auditory oddball sequence is presented over loudspeakers. This sequence consists of spoken syllables that rarely and unpredictably convey a different emotional tone. In one block, frequent syllables are spoken with a neutral prosody and rare ones with an angry or happy prosody, whereas in another block, frequent syllables are spoken with an angry or happy prosody and rare ones are neutral. In accordance with other auditory oddball studies (for a review see Näätänen et al., 2005), a prior ERP study using this paradigm found a mismatch negativity (MMN) when subtracting frequent from rare stimuli. Moreover, the MMN was larger for rare stimuli spoken with an emotional as compared to neutral prosody. These results suggest that auditory change detection, as reflected by the MMN (Näätänen et al., 2005), is enhanced for emotional as compared to neutral events (De Baene et al., 2004; Schirmer et al., 2005).

Using the paradigm described above in the present fMRI study, we predicted that rare changes in tone of voice would activate the primary and secondary auditory cortex. This prediction was derived from prior work that investigated auditory oddball effects using fMRI or optical imaging (Doeller et al., 2003; Tse and Penney, 2007; Tse et al., 2006; Tervaniemi et al., 2006). Oddball effects in this area have been linked to the updating of a sensory memory trace with new, incoming information. Such a process would be expected regardless of whether the incoming information is neutral or emotional. Additionally, we hypothesized that social orientation would enhance the processing of rare emotional as compared to rare neutral prosody. If this were true for perceptual or cognitive processing aspects, we expected to see a correlation between social orientation and fMRI signal changes in regions along the vocal processing pathway in the STS or in the inferior frontal cortex, respectively. Moreover, in line with prior studies, we expected such effects to be lateralized to the right hemisphere (e.g., Fecteau et al., 2007; Wiethoff *in press*; for a review see Schirmer and Kotz, 2006). If social orientation modulates a listener's emotional response to vocal stimuli, correlations between social orientation and fMRI signal changes were expected to show in the OFC and the amygdala. Given the amygdala's presumed role in appraising the relevance of a given stimulus (Sander et al., 2003) finding a correlation between social orientation and amygdala activity would support the proposition that social orientation modulates an individual's emotional response to social signals by enhancing the relevance of these signals.

## Methods

### Participants

Nineteen right handed native German speakers participated in the present experiment. Participants were undergraduate or postgraduate students with no known psychiatric conditions. To prevent potential confounds due to gender differences in social orientation, only one gender was included in the study. Moreover, as the norms provided with the social orientation scale employed in the present study indicated greater variability in the social orientation scores of males as compared to females (Fahrenberg et al., 1994), we selected male participants. Five participants were excluded because of head movements in the scanner. The remaining subjects had a mean age of 26.8 (SD=2.8).

### Material

A female speaker produced the syllables 'dada' several times with angry and neutral prosody. Digital recordings of these syllables were presented to a group of six naïve listeners (three men), who classified each stimulus as either 'very angry', 'angry', 'neutral' or 'emotional' (with the emotion not being anger). These listeners did not participate in the fMRI experiment. Two syllables that had been uniquely identified as 'very angry' and 'neutral' were selected for the subsequent fMRI experiment. Angry and neutral syllables were equally long (557 ms) and loud (67 dB max, 56 dB mean) but differed with respect to fundamental frequency and other frequency formants. Note that the same stimuli have also been used in a previous EEG experiment (Schirmer et al., 2005).

### Experimental design

An experimental session was composed of 8 blocks with 175 frequent ( $p=0.875$ ) and 25 rare events ( $p=0.125$ ) in each block. The emotional and the neutral stimuli served as rare and frequent events in separate blocks. In 4 of the 8 blocks, neutral syllables were the frequent events and emotional syllables the rare events. In the remaining blocks, the emotional syllables were the frequent events and neutral syllables the rare events. The two block types were presented in alternating order. Half the participants started with a block in which the rare events were emotionally spoken syllables whereas the remaining participants started with a block in which the rare events were neutrally spoken syllables. The syllable onset to syllable onset interval in each block was 1.2 s. There was a 20 s period without stimulation between blocks that served to reduce saturation of blood flow changes in response to the experimental stimulation. Participants passively listened to the syllable sequences over headphones while watching a subtitled silent movie (i.e., self-selected episodes of "Wallace and Gromit"). At the end of the experimental session, participants were asked to complete a personality questionnaire, the Freiburger Persönlichkeitsinventar FPI-R (Fahrenberg et al., 1994). This questionnaire contains a social orientation scale that ranges from one (self-centered, self-serving) to nine (socially responsible, helpful to others).

### MRI scanning procedure

The experiment was carried out in a 3 T scanner (Siemens TRIO, Erlangen, Germany). Twenty axial slices (19.2 cm FOV, 64 by 64 matrix, 4 mm thickness, 1 mm spacing), parallel to the AC-PC plane and covering the whole brain were acquired using a single shot, gradient recalled EPI sequence (TR 2000 ms, TE 30 ms, 90° flip angle). One functional run with 1044 repetitions was recorded, with each time point sampled over the 20 slices. Prior to the functional runs, a 20 slice anatomical T1-weighted MDEFT (Uğurbil et al., 1993; Norris, 2000) image (data matrix 256×256, TR 1.3 s, TE 10 ms) and a 20 slice T1-weighted EPI image with the same spatial orientation as the functional data were acquired.

### fMRI data analysis

The fMRI data were processed with the LIPSIA software (Lohmann et al., 2001). This software package contains tools for pre-processing, registration, statistical evaluation, and presentation of fMRI data. Functional data were motion-corrected with the Siemens motion correction protocol (Siemens, Erlangen, Germany) and no further realignment procedure was applied during preprocessing in

LIPSIA. To correct for the temporal offset between the slices acquired in one scan, a cubic-spline interpolation was applied. A temporal high-pass filter with a cutoff frequency of 1/700 Hz was used for baseline correction of the signal. Because we anticipated relatively focal responses in the amygdala, a spatial Gaussian filter set to 5.7 mm FWHM was applied.

To align the functional data slices onto a stereotactic space, a rigid linear registration with six degrees of freedom (3 rotational and 3 translational parameters) was performed. To achieve an optimal match between these images and an individual 3D reference data set (160 slices, 1 mm slice thickness) acquired during a previous scanning session, the parameters were first computed on the basis of the MDEFT and further refined using the EPI-T1 scans (the image in this modality being closer to the EPI functional images). Both the parameters and the 3D reference data set were then normalized to the Talairach stereotactic space (Talairach and Tournoux, 1988). Parameters were then used to resample the functional images using trilinear interpolation (voxel size = 3 × 3 × 3 mm), so that the resulting functional images were normalized to the stereotactic coordinate system. To further reduce interindividual anatomical differences, scans from each participant were subjected to a nonlinear normalization to a 3D reference data set (Thirion, 1998).

The statistical evaluation was based on a least squares estimation using the general linear model for serially autocorrelated observations (see also Friston, 1994; Worsley and Friston, 1995; Aguirre et al., 1997; Zarahn et al., 1997) and a two-stage, random effect analysis (Holmes and Friston, 1998). The design matrix comprised seven experimental regressors, four of which represented the four experimental conditions time locked to event onset. The 100 rare emotional and the 100 rare neutral events served as two regressors, respectively. To equate the number of modelled frequent events with that of available standards, regressors for the frequent events were created by randomly selecting 100 frequent events out of the 1400 available events in the emotional and neutral condition. The frequent events preceding and following a rare event were excluded from this procedure to reduce correlation between frequent event and rare event regressors. Unmodeled emotional and neutral frequent events were added to the model as two additional regressors, as were resting periods between stimulus blocks. In addition to the experimental regressors, six regressors for the movement parameters were included in the model. The data were filtered using a Gaussian kernel (4 s FWHM), the model was con-

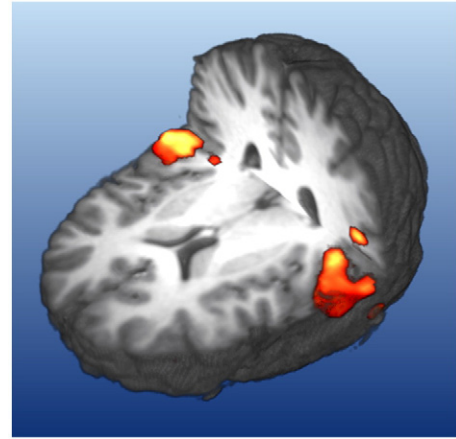


Fig. 1. A contrast between rare and frequent vocalizations revealed activation in the bilateral primary and secondary auditory cortex ( $p < 0.001$ ).

involved with a synthetic haemodynamic response function (Glover, 1999) and the fit between the data and the model was estimated. The following contrast images were computed for each participant and entered into a second level analysis: rare vs. frequent vocalization (both separate for and averaged across emotional and neutral), rare emotional vs. rare neutral vocalizations and frequent emotional vs. frequent neutral vocalizations. To test the hypothesis of a correlation between social orientation and vocal emotional processing, values for the above contrasts were subjected to separate linear regression analyses. These regression analyses were conducted for the whole brain using LIPSIA. They included the individual social orientation scores and a single constant regressor of the average contrast values in the participants. Resulting Z-maps were thresholded at  $Z > 3.09$  ( $p < 0.001$ ). Significant effects from these analyses were reported only if the area of activation extended over 8 or more adjacent voxels. Areas of activation were localized using the Talairach Atlas (Talairach and Tournoux, 1988) and the Duvernoy Atlas (Duvernoy, 1999).

**Results**

*Rare versus Frequent Vocal Expressions*

To investigate the brain correlates associated with the detection of change in speaker tone of voice, we contrasted rare with frequent events by collapsing over emotional and neutral prosody (see Table 1 and Fig. 1). This contrast showed that rare vocalizations elicited larger activity in the primary and secondary auditory cortex as compared to frequent vocalizations ( $x = 62, y = 28, z = 15; x = 61, y = 25, z = 9$ ). Separate contrasts for emotional and neutral prosody indicated that these areas were activated independently of stimulus valence. Moreover, the interaction between tone of voice and frequency was non-significant. An additional analysis with social orientation as a regressor for the comparison between rare and frequent expressions failed to reveal significant effects.

*Emotional versus Neutral Vocal Change*

Brain regions that differentiate between emotional and neutral change in tone of voice were investigated by contrasting emotional and neutral prosody for rare and frequent syllables. Both contrasts failed to reveal any areas that were more strongly activated by emotional as compared to neutral prosody.

Table 1  
fMRI results for the comparison between deviants and standards

Anatomical region	BA	Mean Z	Size	Talairach coordinates		
				x	y	z
<i>Deviant N Standard</i>						
Heschl's Gyrus/STG	41/42	3.46	4320	62	28	15
Heschl's Gyrus/STG	41/42	3.59	3402	61	25	9
<i>Social orientation: Emotional deviant N neutral deviant</i>						
Amygdala		4.41	270	16	10	15
OFC	11	3.70	216	2	29	15
Posterior superior temporal sulcus	21/22	2.59*	189	47	46	6
<i>Social orientation: Emotional standard N neutral standard</i>						
Anterior insula		3.69	297	25	23	3

\* $p < 0.005$ .

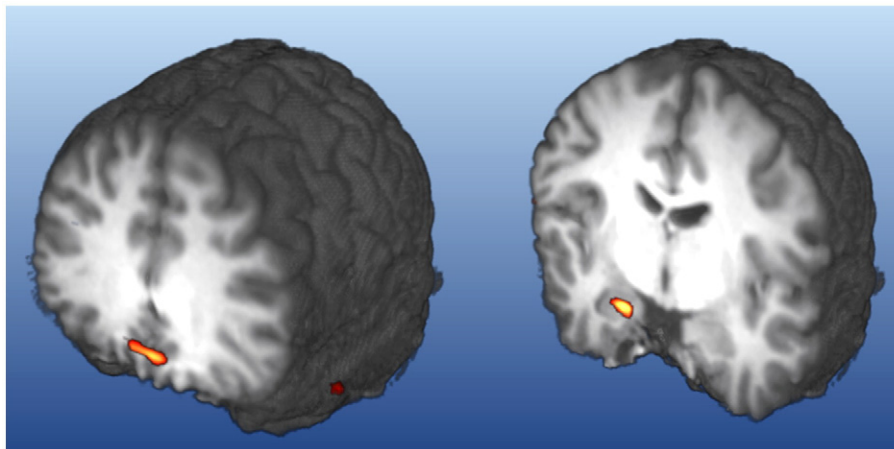


Fig. 2. A positive correlation between social orientation scores and processing differences between rare emotional and rare neutral vocalizations was observed in the right amygdala and the bilateral OFC ( $p < 0.001$ ).

The role of social orientation was explored by conducting a second-level linear regression analysis modeling the relationship between individual social orientation scores and differences in the BOLD-response between rare syllables spoken with emotional and neutral prosody. This analysis revealed that greater social orientation was associated with increased activations to emotional as compared to neutral prosody in the right amygdala ( $x = 16, y = 10, z = 15$ ) and the bilateral OFC ( $x = 2, y = 29, z = 15$ ). A similar tendential effect was seen in the posterior STS with a reduced significance threshold of  $p < 0.005$  ( $x = 47, y = 46, z = 6$ ; see Table 1, Figs. 2 and 3).

Regions of interest analyses were performed to test the observed pattern of lateralization. For the amygdala, we selected two 3-mm spheres centered at the activation peak and its corresponding contra-lateral coordinate, respectively. Because the OFC effect was close to the midline, we selected two spheres placed 7 mm to the left and 7 mm to the right of the midline in the same plane as the peak of activation. Average values for the contrast between emo-

tional and neutral rare syllables were obtained for each sphere and participant and correlated with the participant's social orientation score. Correlations were significant for the right amygdala as well as the left and right OFC (all  $p < 0.05$ ), but were non-significant for the left amygdala ( $p > 0.1$ ). To determine lateralization patterns, we compared the elements in the obtained correlation matrixes using a parametric test, which indicates whether two independent correlation coefficients are significantly different (Steiger, 1980; Olkin and Finn, 1995). This test revealed a significant difference between left and right amygdala ( $Z = 2.83, p < 0.01$ ) but not between the left and right OFC ( $Z < 1$ ).

To test whether the effects observed in the right amygdala and the bilateral OFC were dependent on stimulus frequency, we conducted a further whole brain analysis modeling the relationship between individual social orientation scores and differences in the BOLD-response between frequent syllables spoken with emotional and neutral prosody. This analysis revealed a small area in the anterior insula to be more strongly activated with increasing social orientation ( $x = 25, y = 23, z = 3$ ). No other effects reached significance.

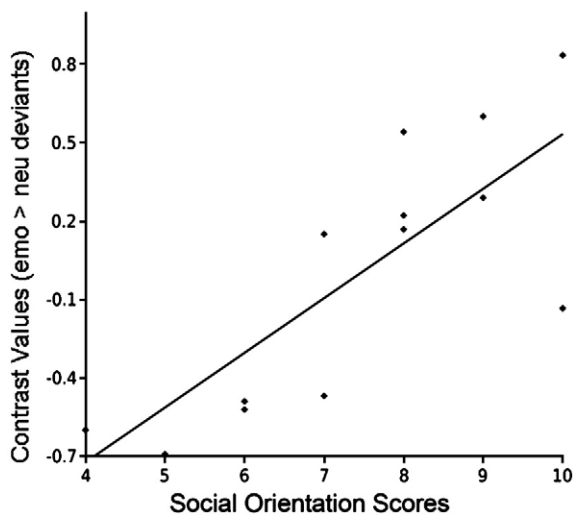


Fig. 3. Scatter plot of the individual contrast values for the contrast between rare emotional and rare neutral vocalizations as a function of social orientation. Mean contrast values were computed for a 9 mm sphere centered around the effect maximum in the right amygdala.

## Discussion

The present study investigated the role of social orientation for the processing of emotional prosody by means of an auditory oddball paradigm. To assess whether our results correspond to previous auditory oddball studies using fMRI, we contrasted rare and frequent events across emotional conditions. In accord with previous work (e.g., Doeller et al., 2003; Rinne et al., 2005), rare acoustic change was associated with activity in the primary and secondary auditory cortex. These areas also correspond to previous ERP work that revealed an MMN effect to rare acoustic change and that localized its source in Heschl's gyrus (Ha et al., 2003). MMN effects mediated by Heschl's gyrus have been interpreted to reflect a basic change detection mechanism that is triggered by any noticeable acoustic change in the environment and that allows humans to respond appropriately. This mechanism is believed to be fairly automatic as it has been evoked in sleeping participants (Martynova et al., 2003) and participants who were engaged in a demanding visual task such as discriminating between rapidly appearing odd and even numbers (Escera et al., 2002).

In addition to indicating change detection, the MMN has also been demonstrated to be sensitive to whether an unattended auditory oddball is emotional or neutral. Emotional oddballs elicit a larger MMN suggesting enhanced change detection (De Baene et al., 2004; Schirmer et al., 2005). The present study investigated the brain structures underlying this enhancement both in a direct contrast between emotional and neutral change as well as in a regression analysis using social orientation scores as a predictor. The direct contrast was non-significant, which likely reflects the influence of interindividual variables on the detection of socially relevant emotional change. Specifically, prior research indicated that male listeners are less likely than female listeners to show enhanced MMN amplitudes to emotional as compared to neutral vocal change (Schirmer et al., 2005). Hence, selecting only male listeners in the present study likely reduced the chance of observing an emotion effect. However, as males show greater variability in social orientation than females (Fahrenberg et al., 1994), the chance of identifying structures that respond to emotional changes in prosody as a function of social orientation were likely to be enhanced in the present sample. Accordingly, a second model with social orientation scores as a predictor for processing differences between rare emotional and neutral prosody revealed activity in the right amygdala and the bilateral OFC. This suggests that enhanced neuronal responses to emotional auditory oddballs are mediated by the amygdala and OFC. Furthermore, we observed increased insular activity to frequent emotional as compared to neutral vocalizations in highly socially oriented individuals. Together these findings corroborate the idea that previously observed interindividual differences in the processing of emotional prosody may be linked to social orientation. In the following paragraphs, we will discuss the potential role of amygdala, OFC, and insula in the processing of emotional prosody and the conclusions that can be derived with regard to the significance of social orientation.

#### *Brain structures implicated in vocal emotional processing*

Previous studies identified a range of structures that respond more strongly to emotional as compared to neutral stimuli. Among these structures are the amygdala and the OFC. Evidence that these structures play a special role in emotion has been found consistently in the visual domain. However, results from auditory studies, in particular studies on the processing of emotional prosody, are equivocal. Here we show that similar to emotive visual stimuli and emotional exclamations, emotionally spoken material may elicit activity in the amygdala and the OFC. The role of these structures in the processing of emotional prosody may be deduced from the conditions that elicited activations in the present study, as well as from previous findings.

In the current study, activity in the right amygdala was observed when social orientation was included in a model that contrasted rare syllables spoken in an emotional and a neutral prosody. This observation is in line with other research suggesting enhanced amygdala response to emotional as compared to neutral stimuli. Moreover, it corresponds to the few prosody and vocal exclamation studies that also activated this structure and that consistently showed lateralization to the right hemisphere. While prior work on emotional prosody activated the right amygdala only (Sander et al., 2006), vocal exclamation studies typically elicited bilateral activity that was stronger in the right as compared to the left hemisphere (Fecteau et al., 2007; Sander and Scheich, 2001). This lateralization pattern is interesting as it contrasts with the preponderance of

left sided activation observed in visual emotion studies (for a review see Baas et al., 2004). Moreover, it points to a specialization of the right hemisphere in vocal emotional processing. Spectral processing – which provides emotional cues based on pitch and voice quality – appears to be lateralized to the right auditory cortex (Zatorre et al., 2002). Strong ipsilateral connections between primary and higher order auditory areas and the amygdala have been identified in the primate brain and are believed to afford a bi-directional exchange of information (Mothe et al., 2006; Yukie, 2002). Hence, a right-lateralization of processing spectral emotional cues may give rise to right lateralized amygdala activation.

Different proposals have been put forward to explain the function of the amygdala in the context of emotional events. Initially, researchers viewed the amygdala as a fear module that facilitates appropriate bodily and behavioral responses to threat (Kjelstrup et al., 2002; Öhman and Mineka, 2001). However, subsequent research revealed that non-threatening negative and positive stimuli also activate the amygdala. For example, amygdala responses were observed to pleasant or disgusting odors (Wicker et al., 2003) as well as to sexually arousing material (Hamann et al., 2004; Stark et al., 2005). Based on this, Sander and colleagues (2003) proposed that rather than subserving a specific emotion, the amygdala may have a more general function in detecting the *relevance* of a particular stimulus for an individual's goals or needs. As goals and needs differ between and within individuals, amygdala responses to a given stimulus are variable. For example, depending on current physiological state, certain stimuli (e.g., food, heat) may be of high or low relevance and engage the amygdala to a greater or lesser extent (Gottfried et al., 2003; O'Doherty et al., 2001). Furthermore, it has been demonstrated that interindividual differences in extraversion affect amygdala responses to happy facial expressions (Canli et al., 2002), suggesting that positive facial cues may be more relevant to an outgoing and excitement seeking individual as compared to an individual that places greater emphasis on internal experiences.

Our results further corroborate the idea of the amygdala serving as a relevance detector. First, we found that rare, but not frequent, emotional vocalization activated the amygdala. Relevance detection is important during the initial encounter with a stimulus but becomes less useful if that stimulus is repeated. The repetition of the same emotional event may trigger other processes including changes in the autonomic state mediated by the anterior insula (Critchley, 2003). In line with this, we observed activity in the anterior insula to frequent emotional as compared to neutral vocalizations. Second, we found that social orientation correlates with amygdala activity elicited by emotional vocalizations. Individuals that were highly interested in social exchange and that strongly cared about other individuals, were more likely to show enhanced amygdala activation in response to unattended and unexpected emotional vocalizations as compared to individuals that were low on these traits. In accordance with previous behavioral evidence (Babchuk et al., 1985; Kitayama and Ishii, 2002; Ishii et al., 2003), these findings likely reflect interindividual differences in the relevance of emotional vocalizations.

The question of what the amygdala does once it detects relevant information was not addressed in the present study. However, one may infer from the literature, that amygdala activation triggers a cascade of responses, including enhanced stimulus processing, attention (Anderson and Phelps, 2001; Vuilleumier et al., 2004) and memory storage (Cahill et al., 1995) – all of which serve to optimize current and future interactions with the stimulus. Accordingly, a tendential effect in the STS and a significant effect in the OFC were

observed in the present study suggesting enhanced processing of emotional as compared to neutral vocalizations. Although the present results allow alternative interpretations, these effects could reflect amygdala dependent modulation of processing.

While STS has been associated with the processing of sensory stimulus aspects, OFC has been implicated in the elicitation of an emotion or feeling state (Hornak et al., 1996; Kringelbach et al., 2003; Lewis et al., 2007). However, as for the amygdala, OFC contribution to the processing of vocal signals has been reported only inconsistently. Based on the results from other modalities, it has been proposed that OFC represents the specific valence of an emotional stimulus – whether a stimulus is good or bad. While this proposal received support from several studies (Zald and Pardo, 2000; Kringelbach and Rolls, 2004; Lewis et al., 2007; Small et al., 2003), the exact neuroanatomical representation of positive and negative valence is still unclear. Some researchers argue for a lateral-medial representation, with more negative stimuli activating lateral and more positive stimuli activating medial cortex (e.g., Kringelbach and Rolls, 2004), whereas others propose a left lateralization for negative valence and a right lateralization for positive valence (e.g., Small et al., 2003). The angrily spoken syllables used in the present study elicited a bilateral, medial OFC activation, which supports neither of the lateralization accounts reviewed here. Although it is beyond the scope of this paper to solve this inconsistency, we propose that a simple bipolar approach to studying OFC function may be inappropriate as there is now accumulating evidence that emotions are represented as individual categories or basic emotions (i.e., fear, anger), based on their behavioral significance and associated bodily states (e.g., Wager et al., 2003).

OFC shares reciprocal connections with the amygdala (Amaral and Price, 1984; Van Hoesen, 1985). Moreover, research in primates revealed an overlap between auditory association cortex and OFC connections in the amygdala and it has been suggested that these three structures form a triadic network (Ghashghaie and Barbas, 2002). Considering this and the presumed relevance detection by the amygdala, one may speculate that emotional prosodic expressions activate an emotional representation in the OFC and that this is a result of temporal lobe processes. However, with respect to the present study we cannot exclude the possibility that OFC representations were activated independently from processes in the amygdala. Future research is necessary to decide between these alternatives.

#### *On the role of social orientation for vocal emotional processing*

Humans differ in the way they interact with their environment. Things that are important to one individual may be irrelevant for another. Psychologists have developed the concept of personality to describe and quantify these differences. Here we show that personality influences how an individual responds to unattended changes in speaker emotion. Specifically, we found that an individual's social orientation was positively correlated with amygdala and OFC responses to vocal emotional change. Based on what is known about these structures, one may conclude that a sudden negative expression from an interaction partner is more likely to activate emotion centers in the brain and to elicit an emotional response in individuals with high as compared to low social orientation. Moreover, one may assume that change in speaker emotion is less likely to go unnoticed if listeners are highly socially oriented. This latter assumption is in line with the research reviewed above demonstrating that the amygdala enhances attention capture and the processing of stimuli

that are of high relevance to an individual's goals or needs (Andersen and Phelps, 2001; Sander et al., 2003; Vuilleumier et al., 2004).

The involvement of amygdala and OFC in highly socially oriented listeners accords with our predictions derived from the literature. However, one may ask whether the observed effects do indeed reflect an increased response to emotionally relevant changes in speaker prosody. Alternatively, they may simply arise from highly socially oriented participants engaging less in the presented movie and devoting more attentional resources to monitoring the vocal sequences. However, this explanation is not very likely as compared to passive oddball designs, active auditory oddball designs enhance activity for rare as compared to frequent events (e.g., Low et al., 2006). Thus, if social orientation increased the likelihood of listeners actively attending to the vocal sequence it should have enhanced brain responses to rare as compared to frequent vocalizations independently of stimulus valence. Importantly, our results failed to support such a general effect of social orientation on attention as a regression model including social orientation and the rare versus frequent event contrast was non-significant.

Taken together, the present findings clearly demonstrate a positive relationship between social orientation and vocal emotional processing. Moreover, they suggest that previously reported effects of gender and culture during vocal emotional processing may be secondary to an underlying influence of social orientation. Social orientation has been shown to differ both between men and women and between individuals from collectivistic and individualistic cultural backgrounds. While social orientation itself is a complex psychological construct that may be subject to a variety of biological (e.g., sex) and environmental (e.g., culture) influences, here we demonstrate that it is nevertheless useful for studying social perception. Measuring social orientation allows researchers to capture the relevance of social information and to predict whether this information will be emotionally engaging.

#### **Acknowledgments**

The data were collected at the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. The authors would like to thank Trevor B. Penney, D. Yves von Cramon, and Barbara Ryan for valuable comments on earlier versions of the manuscript.

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