

Visual Attention Modulates Brain Activation to Angry Voices

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In accordance with influential models proposing prioritized processing of threat, previous studies have shown automatic brain responses to angry prosody in the amygdala and the auditory cortex under auditory distraction conditions. However, it is unknown whether the automatic processing of angry prosody is also observed during cross-modal distraction. The current fMRI study investigated brain responses to angry versus neutral prosodic stimuli during visual distraction. During scanning, participants were exposed to angry or neutral prosodic stimuli while visual symbols were displayed simultaneously. By means of task requirements, participants either attended to the voices or to the visual stimuli. While the auditory task revealed pronounced activation in the auditory cortex and amygdala to angry versus neutral prosody, this effect was absent during the visual task. Thus, our results show a limitation of the automaticity of the activation of the amygdala and auditory cortex to angry prosody. The activation of these areas to threat-related voices depends on modality-specific attention.

Introduction

The automatic detection of potential threat in the environment is vitally important for the organism (LeDoux, 1996). Processing of emotional salient stimuli was proposed to be automatic, i.e., involuntary and independent of attention, and to be associated with activation of specific brain areas, such as the amygdala (LeDoux, 1996; Ohman, 2005). Activation of the amygdala was shown in response to visual threat-related social stimuli, such as threat-related faces (Adolphs et al., 1995; Morris et al., 1996; Zald, 2003; Straube et al., 2004). Amygdalar responses were found even when subjects' attention was distracted from facial expressions (Vuilleumier et al., 2001) or when the presentation of the stimuli was below the threshold of conscious perception (Whalen et al., 2004), supporting the hypothesis of a crucial role of the amygdala in the automatic detection of threat (LeDoux, 1996). However, the assumption of completely automatic amygdalar responses to visual threat was questioned by findings showing the absence of activation in the amygdala and visual areas to threat-related visual stimuli during exhaustion of attentional resources (Pessoa et al., 2002; Bishop et al., 2007; Straube et al., 2007) or when controlling for perceptual (Straube et al., 2010) or experimental artifacts (Pessoa et al., 2005).

In contrast to findings concerning visual threat, such as threat-related facial expressions, there is no evidence that attentional conditions might modulate activation in the amygdala or auditory cortex in response to auditory threat-related stimuli,

such as angry prosody. Several studies showed increased brain responses to angry prosody, even if subjects' attention was distracted from the emotional content (Quadflieg et al., 2008; Ethofer et al., 2009) or the emotional stimulus (Grandjean et al., 2005; Sander et al., 2005). Thus, higher activation of the amygdala and the superior temporal cortex to angry voices was shown regardless of the focus of attention during dichotic listening (Grandjean et al., 2005; Sander et al., 2005) or during the variation of feature-based auditory attention (Quadflieg et al., 2008; Ethofer et al., 2009). These findings have been interpreted as evidence for a mandatory processing of threatening voices (Grandjean et al., 2005).

If responses of the amygdala and auditory areas to angry voices are indeed independent of subjects' attentional focus, activation of these areas should also be observable when subjects' attention is distracted from prosodic stimuli by means of a task that directs attention to another sensory modality than the auditory channel. Cross-modal distraction, such as visual–auditory distraction (Johnson and Zatorre, 2006; Mayer et al., 2009), is a powerful method to modulate activation in sensory regions (Weissman et al., 2004). For example, visual tasks that are unrelated to simultaneously presented auditory stimuli strongly inhibit activation in auditory areas (Johnson and Zatorre, 2006). However, it is unknown whether cross-modal distraction also affects differential brain activation to threat compared with neutral stimuli. Here, we investigated the effect of cross-modal distraction imposed by a visual task on responses of the amygdala and the superior temporal cortex to anger versus neutral prosody.

Materials and Methods

Participants. Twenty-four right-handed healthy subjects (eight female; 16 male; mean age, 22.7 ± 1.49 years) with normal or corrected-to-normal vision participated in the experiments. All participants were right-handed native German speakers and had no history of neurological or psychiatric diseases. Right-handedness was assessed using the Edinburgh Inventory (Oldfield, 1971). Participants provided written in-

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formed consent for the study, which was approved by the ethics committee of the University of Jena.

Stimuli. Prosodic stimuli were evaluated in a previous study (Quadflieg et al., 2008) and consisted of a set of semantically neutral bisyllabic nouns (five letters) spoken in either angry or neutral prosody by two women and two men. Stimuli were recorded and digitized through an audio interface with a 44 kHz sampling rate and a 16 bit resolution. Utterances were normalized in amplitude (70%) and edited to a common length of 550 ms using Adobe Audition 1.5. Furthermore, 20 subjects were instructed to listen to the stimuli and to indicate whether the word was spoken in happy, fearful, surprised, disgusted, angry, sad, or neutral prosody. The evaluation of the stimuli revealed 76.25% (SD, 19.36) correct classification of the anger and 73.16% (SD, 20.16) correct classification of the neutral prosodic stimuli. These results are in line with results of other evaluation studies (Banse and Scherer, 1996; Juslin and Laukka, 2001; Quadflieg et al., 2008; Wiethoff et al., 2009). The two visual stimuli were a centered white cross or circle on a black background.

Experimental design. During scanning, auditory stimuli were presented binaurally via headphones that were specifically adapted for use in an fMRI environment (commander XG MRI audio system; Resonance Technology) and visual stimuli were shown via a back-projection screen onto an overhead mirror. A spoken word and a symbol were presented simultaneously in 16 blocks of 16 trials. Each block started with the visual instruction and a subsequent presentation of a fixation cross, both displayed for 6000 ms. Between blocks, a fixation cross was shown for 4000 ms. In every trial, the spoken word and the symbol were presented for 550 ms followed by a fixation cross for 950 ms. Within the stimulation blocks, the gender of the speaker and the type of symbol were presented in random order. Subjects had to solve an auditory and a visual task, both implemented by a simple two-alternative forced-choice task. Participants had to indicate as fast as possible either the gender of the speaker (auditory task) or the kind of visual symbol (visual task). The auditory condition served as the control condition to ensure that the typical activation to anger prosody in the amygdala and auditory areas was induced by our stimuli. Responses were given via one of two buttons of a fiber optic response box (LUMItouch; Photon Control) with either the index or the middle finger of the right hand. There were four block conditions (auditory task or visual task with either angry or neutral prosody) with four blocks per condition. The order of the blocks was counterbalanced across the participants. Behavioral data were analyzed by means of repeated-measures ANOVA using SPSS software (version 17; SPSS). A probability level of $p < 0.05$ was considered statistically significant. All data are expressed by mean \pm SD.

fMRI data acquisition and analysis. Scanning was performed in a 1.5-T magnetic resonance scanner (Magnetom Vision Plus; Siemens Medical Systems). After acquisition of a T1-weighted anatomical scan, one run of T2*-weighted echo-planar images consisting of 248 volumes was measured (TE, 50 ms; TR, 2980 ms; flip angle, 90°; matrix, 64 \times 64; field of view, 192 mm). Each run was comprised of 30 axial slices (thickness, 3 mm; gap, 1 mm; in-plane resolution, 3 \times 3 mm). The slices were acquired with a tilted orientation to reduce susceptibility artifacts (Deichmann et al., 2003). A shimming procedure was performed before imaging and the first four volumes of each run were discarded from analysis to ensure steady-state tissue magnetization.

Preprocessing and analyses of the functional data were performed with Brain Voyager QX software (Version 1.8.6; Brain Innovation). At first, all volumes were realigned to the first volume. Further data preprocessing comprised spatial (8 mm full-width half-maximum isotropic Gaussian kernel) as well as temporal smoothing (high-pass filter, 3 cycles per run; linear trend removal). The anatomical and functional images were coregistered and normalized to the Talairach space (Talairach and Tournoux, 1988).

Statistical analyses were performed by multiple linear regression of the signal time course at each voxel. The expected blood oxygen level-dependent (BOLD) signal change for each event type (predictor) was modeled by a hemodynamic response function. Within-group statistical comparisons were conducted using a mixed-effect analysis. In the first step, predictor estimates were generated for each individual. In the second step, predictor estimates were analyzed across subjects. The analysis

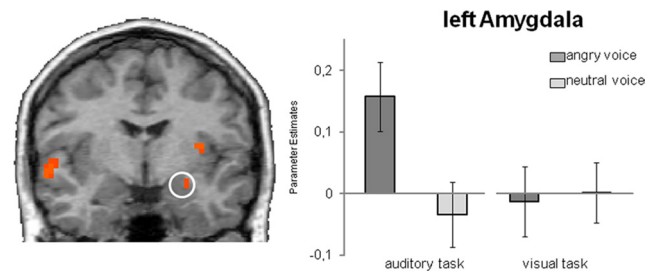


Figure 1. Higher activation of the left amygdala to angry voices in the auditory task but not in the visual task. Statistical parametric maps are overlaid on an averaged T1 scan (radiological convention: left = right; $y = -6$). The plots show the difference of parameter estimates (angry vs neutral voices; mean and SE).

was conducted in regions of interest (ROI; superior temporal region, including the superior temporal gyrus, superior temporal sulcus, and amygdale), which showed automatic responses to angry prosody in previous studies, and exploratory for the whole brain. ROIs were defined with help of Talairach daemon software (Lancaster et al., 2000) and according to our previous studies (Straube et al., 2004, 2005, 2010; Quadflieg et al., 2008). Statistical parametric maps resulting from the voxelwise analysis were considered significant for statistical values that survived a cluster-based correction for multiple comparisons as implemented in Brain Voyager (Goebel et al., 2006), which is based on a 3D extension of the randomization procedure described by Forman and colleagues (1995). First, voxel-level threshold was set at $p < 0.005$ (uncorrected). Thresholded maps were then submitted to a ROI- or whole brain-based correction criterion that was based on the estimate of the map's spatial smoothness and on an iterative procedure (Monte Carlo simulation) for estimating cluster-level false-positive rates. After 1000 iterations, the minimum cluster size threshold that yielded a cluster-level false-positive rate of 5% was applied to the statistical maps.

Results

Performance data

Analyses of reaction times revealed a significant effect of task ($F_{(1,23)} = 113.63, p < 0.05$), with faster reaction times in the visual task (auditory task: 684.23 ± 141.61 ms; visual task: 508.46 ± 97.77 ms). Critically, there was no effect of prosody ($F_{(1,23)} = 0.93, p = 0.344$) and no interaction of task by prosody ($F_{(1,23)} = 0.31, p = 0.58$). Analyses of error rates revealed a significant effect of task ($F_{(1,23)} = 20.04, p < 0.05$), with higher error rates in the auditory task (auditory task: $7.94 \pm 5.83\%$; visual task: $3.97 \pm 5.11\%$). Critically, there was no significant effect of prosody ($F_{(1,23)} = 2.82, p = 0.11$) and no interaction of task by prosody ($F_{(1,23)} = 0.17, p = 0.68$).

fMRI data

Auditory task

We found increased activation to angry versus neutral voices in the left amygdala (peak $x, y, z: -23, -6, -12; t_{(23)} = 3.16, p < 0.05$, corrected) (Fig. 1) and bilateral in the superior temporal region (left: peak $x, y, z: -51, -10, -3; t_{(23)} = 3.19, p < 0.05$, corrected; right: peak $x, y, z: 50, -11, 6; t_{(23)} = 4.05, p < 0.05$, corrected) (Fig. 2). There was also above-threshold activation in the right amygdala on the voxel level. However, this cluster did not meet the required cluster threshold. Additional exploratory whole-brain analysis revealed only one cluster in the left insula (peak $x, y, z: -32, -3, 12; t_{(23)} = 4.16, p < 0.05$), indicating higher activation to angry versus neutral voices. Furthermore, findings were not dependent on the speakers' or the participants' gender. Thus, there was no significant difference between male and female speakers for the contrast angry versus neutral prosody and there was also no effect of participants' gender on the results

and no interaction between the speakers' and the participants' gender.

Visual task

During the visual task, no increased activation to angry versus neutral prosody was detected in the ROIs (for illustration of the BOLD response depending on the focus of attention, see Figs. 1, 2). Exploratory whole-brain analysis also revealed no areas of increased activation to angry versus neutral prosody.

Auditory task versus visual task

Direct comparisons between tasks confirmed that activation was significantly increased in the left amygdala (peak x, y, z : $-23, -4, -9$; $t_{(23)} = 3.13, p < 0.05$, corrected) and left (peak x, y, z : $-58, -32, 6$; $t_{(23)} = 3.24, p < 0.05$, corrected) and right (peak x, y, z : $50, 7, -14$; $t_{(23)} = 3.24, p < 0.05$, corrected) superior temporal cortex.

Discussion

The present study investigated brain responses to angry versus neutral prosody in a cross-modal distraction paradigm. We found higher activation to angry versus neutral prosody in the amygdala and in the superior temporal region in the auditory task. This effect was completely absent when the focus of attention was directed to the visual modality, suggesting that visual distraction may inhibit the preferential processing of anger prosody.

This finding is in contrast to previous studies that used auditory unimodal distraction designs, like a dichotic listening paradigm (Grandjean et al., 2005; Sander et al., 2005). These studies showed higher activation to angry prosody in the amygdala and the superior temporal cortex, regardless of the attended ear. Moreover, Quadflieg et al. (2008) and Ethofer et al. (2009) also showed higher activation of the amygdala and the superior temporal cortex to angry versus neutral prosody regardless of attentional conditions.

Prosodic features are powerful signals during interpersonal contact since they enable the reliable discrimination and identification of a speaker's emotional state (Frick, 1985; Banse and Scherer, 1996). Angry voices, in particular, signal rejection and threat (Frick, 1985; Banse and Scherer, 1996). Growing evidence indicates that a network that is spatially distributed across both hemispheres contributes to the appropriate comprehension of emotional prosody (Imaizumi et al., 1997; Adolphs et al., 2002; Kotz et al., 2003; Belin et al., 2004; Wildgruber et al., 2005; Schirmer and Kotz, 2006). Above all, a bilateral frontotemporal pattern of brain activation was shown to be associated with processing emotional prosody from normal speech (Kotz et al., 2003).

While it is assumed that the superior temporal region, which was activated during our auditory task, serves as an input region mainly involved in the fast and more or less automatic analysis of acoustic features, subsequent processes that are more complex and integrative in nature, such as labeling the affective tone and/or retrieving its reward value, are thought to be accomplished by bilateral frontal brain regions (Hornak et al., 1996; Kotz et al., 2003; Belin et al., 2004; Wildgruber et al., 2004, 2005; Ethofer et al., 2006; Peelen et al., 2010). Since activations in these frontal areas are related to explicit emotional tasks or higher emotional appraisal (Sander et al., 2005; Quadflieg et al., 2008; Peelen et al., 2010), the implicit auditory task used in the present study was not suited to activate these areas. The activation of the insula found in the

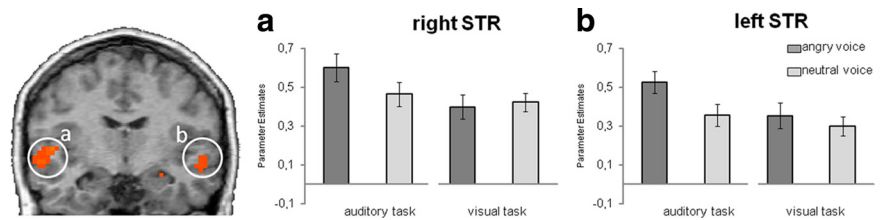


Figure 2. Higher activation of the right (**a**) and left (**b**) superior temporal region (STR) to angry voices in the auditory task but not in the visual task. Statistical parametric maps are overlaid on an averaged T1 scan (radiological convention: left = right; $y = -10$). The plots show the difference of parameter estimates (angry vs neutral voices; mean and SE).

exploratory analysis is in accordance with previous work (Quadflieg et al., 2008). It has been suggested that the insula might be associated with threat evaluation due to the processing of threat-related bodily responses (Critchley et al., 2004; Straube et al., 2006).

The role of the amygdala might be found in rapid detection of emotional input. As suggested for the visual modality (Amaral et al., 2003; Freese and Amaral, 2005), the amygdala may have substantial modulatory control over sensory processing in the auditory modality due to back projections to sensory areas (Yukie, 2002). Thus, the amygdala may increase activity in auditory cortex according to the affective saliency of stimuli and, correspondingly, enhance auditory representation and processing of the target objects (Sander et al., 2005; Scharpf et al., 2010). The present study found a significant activation of the left amygdala, while the activation of the right amygdala did not survive the control for multiple comparisons. This finding, even though representing only a threshold effect, might be due to our verbal stimulus material.

Our data reveal that neither activation in the superior temporal cortex nor the amygdala is immune to distraction. Generally, our data are in accordance with findings from the visual modality showing the limitation of automatic brain responses to visual threat (Pessoa et al., 2002; Bishop et al., 2007). In these studies, the variation of perceptual load by means of a demanding task, which is presented either peripheral (Pessoa et al., 2002) or central (Bishop et al., 2007) to fixation, led to the exhaustion of processing capacity. However, in contrast to these studies, our results cannot be explained by effects of task difficulty per se. Performance data did not indicate that the visual task was more difficult than the auditory task.

However, our results could be explained by cross-modal inhibition of sensory cortices (Weissman et al., 2004; Johnson and Zatorre, 2006; Mayer et al., 2009) and visual dominance (Posner et al., 1976). Johnson and Zatorre (2006), for example, showed increased activity in the task-relevant sensory cortices and an inhibition of the activation of the cortex associated with the unattended modality during visual–auditory distraction. Thus, in the visual task in our study, the differential analyses of emotional voices might have been suppressed and no further processing occurred, including activation of the amygdala. Furthermore, Posner et al. (1976) suggested that visual attention is associated with cognitive effort and blocks the processing of stimuli from other modalities. Thus, even the simple visual task in our design might provide a relatively high attentional load, which additionally accounted for the absence of differential neural processing of angry versus neutral voices.

It should be noted that we do not propose that visual distraction inhibits processing of emotional prosody under all conditions. Specific task configurations such as switching between sensory modalities might potentiate the cross-modal distraction effect. Future studies might compare different paradigms and,

for example, use experimental designs with varying attentional load imposed by a visual task while prosodic stimuli are presented simultaneously. Regardless of the exact mechanisms of how the processing of emotional information is blocked, the current findings support the view that there is no obligatory pathway for the processing of threat-related stimuli, but that cognitive resources (Pessoa and Adolphs, 2010), the emotional context (Dolan et al., 2001), or the saliency of threat-related stimuli (Mothes-Lasch et al., 2009) strongly modulate brain responses to these stimuli.

Together, our results question the hypothesis that there is an automatic activation of the amygdala and the auditory cortex to angry prosody regardless of attention. Rather, it depends on the sensory modality of the attentional focus, since attending to the visual modality prevented activation to angry versus neutral prosody in the amygdala and superior temporal cortex. This finding suggests that cross-modal distraction represents a powerful method to test limits of automatic processing of threat stimuli.

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