



## Research report

# The brain's relevance detection network operates independently of stimulus modality

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## ABSTRACT

Brain regions associated with the processing of emotional stimuli are often also associated with the processing of social stimuli. Therefore, this network consisting of the amygdala, the anterior insula, the superior temporal sulcus (STS), and the orbitofrontal cortex (OFC) may rather be involved in more general relevance detection which should be independent of the sensory modality of the stimuli. In the current study, we used functional MRI to measure brain activations while participants either viewed pictures that varied in their emotional and social content or listened to sounds that varied along the same dimensions. The amygdala, the anterior insula, the STS, and the OFC showed increased activation during processing of emotional as well as social stimuli independent of the sensory modality in which the stimuli were presented. Moreover, social emotional stimuli elicited more pronounced activity in this network than stimuli with solely emotional or social content. These results indicate that the proposed network involved in relevance detection works independently of the source of relevance (emotional or social information mediated by the stimulus) and modality.

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## 1. Introduction

One of the most important functions of the human brain is to register and selectively respond to those stimuli in the environment that are of significance for the organism. Stimulus significance can be determined by stimulus features such as intensity or novelty, but also by their emotional relevance, e.g. being capable to elicit an emotional response. Moreover, emotionally evocative stimuli often also have a social reference [8,24]. Socially generated emotional stimuli motivate people to act in social interactions, e.g. a smile stimulates a smile, a verbal attack provokes a defensive or aggressive response and the hope of a future social incentive, e.g. to get a promotion, increases the effort put into work. This interpersonal character of emotions gained more and more attention in recent years. Emotions help to coordinate social interactions through their informative, evocative, and incentive functions [16]. Thus, one could argue that brain areas critical for processing of emotionally relevant stimuli might also be involved in the processing of the social relevance of external stimuli.

Adolphs and Spezio proposed a neural network for social cognition including cortical (e.g. the orbitofrontal cortex (OFC) and the

primary visual cortex) and limbic structures (e.g. the amygdala and the insula), that are also critically involved during processing of emotionally relevant stimuli [1]. According to this model, the amygdala plays a critical role in this network as it modulates the activity in other parts of the network [35,38]. Increased activation of the amygdala has reliably been found during processing of both unpleasant (including fear evoking) and pleasant stimuli in numerous functional brain imaging studies [9,11,20,27,37]. Moreover, increased activation of the amygdala has also been found during social cognition, e.g. during processing of emotional facial expressions [7,36], in the evaluation of trustworthiness in faces of unknown people [2,39] and in the processing of novel neutral faces compared to repeatedly shown neutral faces [40]. These data suggest that the amygdala is involved in more general relevance detection rather than specifically in emotion processing (cf. [29]). The amygdala not only has connections to subcortical regions including the brain stem but also to several cortical areas [3] putting this structure forward as an ideal candidate for a first stage relevance detector.

Although many studies investigated brain responses to emotional vs. neutral and to social vs. non-social stimuli only few studies explored the interaction between both dimensions. Using pleasant, neutral, and unpleasant pictures from the International Affective Picture System (IAPS [19]) divided into social (pictures that contained faces and bodies) and non-social (objects and animals) stimuli, a clear interaction between processing of social and

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emotional information in the STS, the middle occipito-temporal cortex, and the thalamus was observed [24]. Emotional pictures with socially relevant information evoked stronger activation in these regions than all other groups of pictures. The authors interpreted this interaction as a synergistic effect of social and emotional cues grabbing more natural selective attention [18]. In contrast, the amygdala was activated additively, not interactively, by social and emotional information, supporting the hypotheses that the amygdala appears to be primarily involved in relevance detection, regardless of the nature of the relevance (i.e. social or emotional relevance). Another study [8] combined film clips with static pictures varying along the social and the emotion (valence) dimension. Amygdala activity was associated with both dimensions, while only the social emotions (joy and sadness) activated the superior temporal gyrus. Therefore, both studies clearly underscore that those brain regions involved in the processing of emotional stimuli are also modulated by the social relevance of these cues, either interactively or additively. In the current study, we extended this work by using both visual and auditory stimuli and investigated the effect of social information embedded within emotionally evocative stimuli.

Functional brain imaging studies also reported increased amygdala activation to emotional human sounds [15,30]. Enhanced responses to emotional vocalizations were also found in the anterior insula [23] and the prefrontal cortex [12]. In addition, emotional compared to neutral prosody was found to elicit increased responses in voice specific areas of the middle superior temporal sulcus [14]. Thus, significant auditory stimuli seem to be processed in the same neural networks that are described by the model of Adolphs and Spezio developed for visual stimuli [1]. The first study that compared brain responses to both visual and auditory emotional stimuli found increased amygdala activation to emotional pictures and sounds [4]. The current study follows up on this research and subdivided emotional and neutral visual and auditory stimuli into those that convey social information and those which do not. If the neural networks described above are indeed specialized for extracting emotionally and socially relevant information from the environment, this capacity should be independent of the sensory modality of the stimuli.

## 2. Methods

### 2.1. Participants

Twenty-four healthy female students (age range 19–31 years) of the University of Greifswald participated in the study and received course credits for participation. Participants were randomly assigned either to passively view visual ( $N=12$ ) or to passively listen to auditory ( $N=12$ ) stimulus materials. A between-design was chosen to reduce the length of the experiment to reduce the influence of fatigue. All participants gave their written informed consent to the experiments approved by the University of Greifswald ethics committee.

### 2.2. Stimulus materials and design

Visual stimuli were 144 pictures selected from the International Affective Picture System (IAPS [19])<sup>2</sup>. There were 48 pleasant, neutral and unpleasant pictures

<sup>2</sup> IAPS identification numbers: pleasant/social: 4670, 4659, 4531, 4460, 4681, 4652, 4660, 4800, 4664, 4810, 4650, 4683, 2550, 2345, 2501, 8461, 2311, 2340, 2391, 2360, 2530, 2341, 2310, 2050; pleasant/non-social: 8190, 5621, 8080, 8162, 5623, 7501, 8170, 5460, 5629, 8400, 8200, 8034, 1610, 5910, 1920, 7502, 1460, 5700, 1440, 5982, 1710, 5760, 1750, 7580; neutral/social: 2190, 2570, 2516, 2215, 2385, 2280, 2480, 2214, 2200, 7700, 7491, 7640, 7211, 7224, 7234, 7560, 7190, 7495, 7705, 7620, 7496 (and also 3 pictures of neutral facial expressions from the Karolinska Directed Emotional Faces (KDEF) Archive [22]); neutral/non-social: 7160, 7238, 7182, 7187, 7830, 7184, 7185, 7096, 7237, 7183, 7186, 7820, 7080, 7025, 7010, 7009, 7150, 7002, 7235, 7004, 7950, 7090, 7006, 7110; unpleasant/social: 6350, 3000, 9252, 3170, 6313, 3080, 9410, 3030, 3530, 6540, 9433, 3500, 2800, 2205, 9041, 2700, 9421, 3220, 3350, 2141, 3230, 9220, 2900, 3300; unpleasant/non-social: 9910, 9620, 6230, 9921, 6210, 9611, 6260, 9920, 9050, 6250, 9630, 6300, 9300, 7380, 9373, 9340, 9180, 1275, 9390, 9830, 9182, 9280, 9290, 9140.

each that were further divided into those pictures depicting persons and faces (24 pictures with social information within each category) and those pictures depicting non-human scenes, objects, and animals (24 pictures without any socially relevant information within each category). Auditory stimuli were 72 sounds selected from the International Affective Digitized Sounds Archive (IADS [6])<sup>3</sup>. The stimuli were selected based on the both gender normative rating (as rated with the 9 point self-assessment-manikin-scale) so that the resulting stimulus set complied with the following requirements: (1) picture and sound stimuli did not differ significantly according to their valence ratings ( $t(2, 160)=0.072$ , ns; mean normative ratings given for pictures: valence: pleasant = 7.28, neutral = 5.01, unpleasant = 2.37; sounds: valence: pleasant = 7.11; neutral = 5.05, unpleasant = 2.63) and (2) social and non-social stimuli also did not differ significantly in their valence and arousal ratings (valence:  $t(2, 219)=1.48$ , ns; arousal:  $t(2, 219)=0.97$ , ns; corresponding means: social: valence: pleasant = 6.99, neutral = 4.91, unpleasant = 2.19, arousal: emotional = 5.99, neutral = 3.97; non-social: valence: pleasant = 7.47; neutral = 5.15, unpleasant = 2.75, arousal: emotional = 5.88, neutral = 3.41). Finally, emotionally evocative stimuli (pleasant and unpleasant) did not differ irrespective of whether they conveyed socially relevant information or not (pictures:  $t(2, 97)=1.20$ , ns; sounds:  $t(2, 54)=0.67$ , ns).

Pictures of each category (e.g. unpleasant/social) were presented for 3 s in a 12 s block of four pictures. Sounds of each category were presented for 6 s in a 12 s block of two sounds. Between these blocks a white fixation cross was presented on a black screen for 12 s forming the inter-block-intervals. Six blocks of each content category (unpleasant/social, unpleasant/non-social, neutral/social, neutral/non-social, pleasant/social, pleasant/non-social) were presented in a randomized order. Category exemplars were selected by a PC-shuffle device so that each participant viewed a different order of individual stimuli. Stimulus presentation was controlled by Presentation software (Neurobehavioral Systems). Pictures were back-projected onto a translucent screen and were viewed by participants through a mirror affixed at the head coil. Sound stimuli were presented via pneumatic headphones.

### 2.3. Apparatus and image acquisition

MRI data were collected using a 1.5 T Magnetom Symphony system (Siemens) that was additionally equipped with an 8-channel-headcoil. Before starting with the recording sequences, field-homogeneity was optimized by a shimming-sequence. After aligning the images in a transversal plane parallel to the AC-PC-line on basis of a localizer scan, a T1-weighted anatomical volume (TE = 4.88 ms, flip angle = 40, FoV = 192 mm, matrix = 256 × 256, voxel size = 1 mm × 1 mm × 1 mm) was recorded. During stimulus presentation 294 echo-planar images were acquired using 33 slices (3 mm thick, 0.75 mm gap) per volume (EPs; TR = 3000 ms, TE = 50 ms, flip angle = 90, FoV = 192 mm, matrix = 64 × 64, voxel size = 3 mm × 3 mm × 3 mm).

### 2.4. Image processing and data analysis

Preprocessing and statistical analyses were realized using the statistical parametric mapping software (SPM5, Wellcome Department of Imaging Neuroscience, London, UK). Preprocessing included spatial realignment, co-registration, normalization into the MNI space, and spatial smoothing (FWHM 12 mm). To correct for low-frequency components, a high-pass filter with a cut off of 128 s was used. Statistical analyses were performed using the general linear model as implemented in SPM5. For each participant a design matrix was created using a canonical hemodynamic response function for each of the six content categories and for the inter-block periods. The 6 movement parameters estimated during the realignment procedure were introduced as covariates into the model to control for the variance due to head displacements. Preliminary 2nd level analyses revealed no significant differences between pleasant and unpleasant categories in either of the both stimulus modalities. Therefore, individual statistical maps (fixed effects) were calculated for the main effects (1) emotional vs. neutral, (2) social vs. non-social used for 2nd level one-sample- $t$ -tests and for the effects (3) neutral/social vs. neutral/non-social, and (4) emotional/social vs. emotional/non-social used for the interaction contrast ((emotional/social > emotional/non-social) > (neutral/social > neutral/non-social)) that was conducted by means of a 2nd level paired  $t$ -test. The statistical threshold used to report group-activations was set at  $p < 0.05$  corrected for the whole brain (false discovery rate; FDR [13]) and with an extent threshold of ten contiguous voxels. The  $t$ -values of significant activations of the highest activated voxels were given for the MNI-coordinates and were assigned to anatomical regions.

Statistical thresholds for region-of-interest-analyses (amygdala, anterior insula, superior temporal sulcus (STS), and orbitofrontal cortex (OFC), and the primary

<sup>3</sup> IADS identification numbers: pleasant/social: 215, 201, 205, 216, 202, 200, 210, 110, 226, 221, 220, 230, 112, 109; pleasant/non-social: 360, 352, 353, 351, 401, 362, 206, 816, 601, 820, 810, 815, 802, 812; neutral/social: 262, 720, 311, 310, 251, 252, 723, 358, 320, 425, 325, 708, 361, 700; neutral/non-social: 704, 113ird, 100ir, 722r, 701ird, 826d, 370d (i = inverted, r = reverted, d = delayed), 171, 132, 602, 105, 152, 120, 113; unpleasant/social: 279, 285, 278, 277, 276, 286, 290, 291, 280, 711, 292, 261, 423, 287; unpleasant/non-social: 600, 424, 422, 625, 698, 712, 709, 106, 115, 116, 627, 130, 500, 133.

**Table 1**  
Summary of results for the main contrast emotional vs. neutral of visually and auditory evoked BOLD-activity with significant activated regions, MNI-coordinates, and cluster size ( $k_E$ ).

Region/Brodman areas (BA)	MNI			$k_E$	$t$ -score	Region/Brodman areas (BA)	MNI			$k_E$	$t$ -score		
	x	y	z				x	y	z				
Pictures						Sounds							
Emotional > neutral						Emotional > neutral							
Whole-brain ( $p_{FDR} < 0.05$ )													
Middle temporal gyrus	R	45	-63	3	5648	14.15	Superior temporal gyrus (BA 21)	L	-60	-3	-6	496	21.47
Anterior insula (BA 47)	R	27	12	-21	139	5.52	Superior temporal gyrus	R	57	-33	6	267	9.41
Anterior insula (BA 47)	R	48	15	-3	59	5.11	Inferior frontal gyrus	L	-39	24	-6	43	7.92
Thalamus (Pulvinar)	L	-21	-30	3	115	4.63	Posterior cingulate gyrus (BA 23)	R	3	-51	24	24	7.23
Superior parietal gyrus	R	27	-57	69	22	4.30	Superior temporal pole	R	42	15	-24	11	5.31
Supramarginal gyrus	R	60	-36	36	53	4.15							
Supramarginal gyrus	L	-60	-33	30	13	3.34							
Thalamus	R	15	-33	0	46	4.07							
Anterior insula	L	-45	15	-3	14	4.05							
Hippocampus	L	-30	-9	-24	14	3.77							
Precuneus	R	3	-60	63	18	3.58							
Regions-of-Interest ( $p_{uncorr.} < 0.005$ )													
Primary visual cortex	L	-18	-93	12		9.60	Primary auditory cortex	L	-54	-24	9		6.43
	R	9	-96	6		8.09		R	60	-15	9		4.64
Amygdala	L	-27	-3	-24		3.66	Amygdala						
	R	30	-3	-18		4.28		R	21	-6	-12		3.28
Anterior insula	L	-45	15	-3		4.05	Anterior insula	L	-39	24	-6		7.92
	R	27	12	-21		5.52							
STS	L	-51	-63	3		6.56	STS	L	-54	-18	-3		9.70
	R	57	-57	6		4.68		R	57	-33	6		9.41
OFC	L	-45	15	-6		3.45	OFC	L	-39	24	-6		7.92
	R	30	15	-24		4.82		R	36	24	-18		3.96

STS, superior temporal sulcus; OFC, orbitofrontal cortex.

**Table 2**  
Summary of results for the main contrast social vs. non-social of visually and auditory evoked BOLD-activity with significant activated regions, MNI-coordinates, and cluster size ( $k_E$ ).

Region/Brodman areas (BA)	MNI			$k_E$	$t$ -score	Region/Brodman areas (BA)	MNI			$k_E$	$t$ -score		
	x	y	z				x	y	z				
Pictures						Sounds							
Social > non-social						Social > non-social							
Whole-brain ( $p_{FDR} < 0.05$ )													
Anterior insula/amygdala	R	30	9	-18	118	10.77	Middle temporal gyrus	L	-51	-21	-12	1764	12.29
Middle temporal gyrus	R	36	-51	9	532	9.53	Rolandic operculum	R	42	-18	21	1209	8.02
Middle occipital gyrus	L	-51	-72	-3	810	8.98	Anterior cingulate gyrus	R	9	33	3	36	6.05
Hippocampus	L	-12	-12	-12	340	8.35	Anterior cingulate gyrus	L	-6	9	29	186	5.58
Inferior temporal gyrus	L	-42	-45	-18	178	7.99	Precentral gyrus	R	45	-12	48	24	5.45
Medial temporal gyrus	L	-57	-6	-21	46	7.89	Medial frontal gyrus	L	-9	51	18	223	4.91
Medial temporal pole	L	-51	15	-33	15	5.29	Middle frontal gyrus	R	36	-3	57	28	4.74
Medial frontal gyrus (BA11)	L	-3	57	-15	25	4.71	Middle temporal gyrus	R	45	-66	21	26	4.62
Superior frontal gyrus (BA9)	L	-6	51	27	43	4.49	Inferior frontal gyrus	L	-36	18	21	21	4.33
							Anterior insula (BA 13)	L	-42	12	3	10	4.24
Regions-of-interest ( $p_{uncorr.} < 0.005$ )													
Primary visual cortex	L	-21	-99	-6		3.28	Primary auditory cortex	L	-51	-24	6		4.17
								R	45	-21	6		6.84
Amygdala	L	-30	-6	-15		4.34	Amygdala	L	-24	-6	-12		5.30
	R	27	3	-18		7.79		R	27	-3	-27		3.88
Anterior insula	L	-33	12	12		3.23	Anterior insula	L	-30	18	-12		4.67
	R	30	9	-18		10.77		R	27	12	-6		3.27
STS	L	-57	-6	-21		7.89	STS	L	-51	-18	-12		10.77
	R	54	-51	9		4.18		R	48	-42	12		5.04
OFC	L	-3	57	-15		4.41	OFC	L	-36	24	-9		5.08
	R	30	15	-24		5.06		R	12	39	-3		4.17

STS, superior temporal sulcus; OFC, orbitofrontal cortex.

**Table 3**

Results for the region-of-interest-analyses of the interaction contrast (emotional/social > emotional/non-social) > (neutral/social > neutral/non-social) of visually and auditory evoked BOLD-activity.

Region		MNI			t-score*	Region	Side	MNI			t-score*
		x	y	z				x	y	z	
Pictures						Sounds					
(Emotional/social > emotional/non-social) > (Neutral/social > neutral/non-social)						(Emotional/social > emotional/non-social) > (Neutral/social > neutral/non-social)					
Primary visual cortex	L/R	0	−93	3	5.86	Primary auditory cortex	L	−51	−30	9	3.52
							R	60	−15	9	4.21
Amygdala	R	21	6	−18	5.46	Amygdala					
Anterior insula	L	−30	18	−18	7.00	Anterior insula	L	−33	18	0	4.73
	R	27	15	−18	10.24		R	30	12	−12	5.17
STS	L	−54	−63	3	8.91	STS	L	−57	−27	−3	5.85
	R	57	−57	6	6.20		R	48	−27	−3	6.15
OFC	L	−33	21	−12	6.09	OFC	L	−36	24	−9	4.37
	R	24	15	−18	7.14		R	42	30	−9	3.98

\*  $p_{\text{uncorr.}} < 0.005$ ; STS, superior temporal sulcus; OFC, orbitofrontal cortex.

sensory cortices) were set at 0.005, uncorrected. Amygdala, anterior insula, OFC, and the primary sensory cortices were identified using the “Automated Anatomical Labelling” software (AAL [34]). As the AAL does not include a mask for the superior temporal sulcus (STS), an area 4 mm superior and inferior to the superior temporal sulcus and restricting the anterior–posterior ( $y$ -) direction from  $-20$  to  $-60$  was selected, which covers the findings of eye, hand and mouth representation in prior publications [21,25].

### 3. Results

#### 3.1. Brain activation during viewing of emotional and social pictures

##### 3.1.1. Whole-brain-analysis

Viewing of emotionally relevant pictures evoked stronger activation than viewing of neutral pictures in the extrastriate visual cortical areas (maximum activation in the middle temporal gyrus) as well as in the anterior insula, the thalamus, the superior parietal gyrus, the supramarginal gyrus, the hippocampus, and the precuneus. Compared to emotionally evocative pictures, neutral pictures only evoked stronger activation in the inferior parietal gyrus (BA 40). Compared to non-social scenes, pictures of persons and faces evoked stronger activations in the amygdala, the anterior insula, several regions of the temporal and frontal lobe and the middle occipital lobe (see Tables 1 and 2). Pictures without socially relevant information did not show stronger activation in any brain region if contrasted to social pictures.

##### 3.1.2. Region-of-interest analysis

**3.1.2.1. Primary visual cortex.** As expected, viewing of emotional pictures evoked stronger activity in the bilateral striate visual cortex relative to viewing of neutral pictures (see Table 1 and Fig. 3). Viewing of social pictures led to increased BOLD-signal in the left primary visual cortex compared to viewing of non-social visual stimuli (see Table 2 and Fig. 3). The interaction contrast revealed that the primary visual cortex was most strongly activated by pictures that had both emotional and social content (see Table 3).

**3.1.2.2. Amygdala.** Viewing of emotional pictures also elicited more pronounced BOLD-responses within the amygdala than viewing of pictures with neutral contents (see Table 1 and Fig. 1). Viewing of socially relevant pictures also evoked more pronounced amygdala activation than viewing of pictures with non-social contents (see Table 2 and Fig. 1). Emotional pictures depicting humans evoked more pronounced activity in the right amygdala than any other picture category (see Table 3).

**3.1.2.3. Anterior insula.** As expected, viewing of emotionally relevant pictures elicited significantly stronger activation in the anterior insula compared to viewing of neutral pictures (see Table 1 and Fig. 1). Viewing of visual stimuli depicting humans and faces also produced more pronounced anterior insula activation than viewing pictures with non-social contents (see Table 2 and Fig. 1). The interaction contrast revealed that viewing of emotional social pictures resulted in the most pronounced bilateral insula activation (see Table 3).

**3.1.2.4. Superior temporal sulcus.** Viewing of emotional pictures elicited more pronounced STS-activation than viewing of neutral pictures (see Table 1 and Fig. 1). As expected, viewing pictures with social content also produced more STS-activation than viewing pictures with non-social contents (see Table 2 and Fig. 1). Emotional social pictures evoked more pronounced bilateral STS-activation than any other picture category (see Table 3).

**3.1.2.5. Orbitofrontal cortex.** Viewing of emotional pictures elicited more pronounced BOLD-responses in the OFC than viewing of neutral pictures (see Table 1 and Fig. 1). Social visual stimuli also evoked more bilateral OFC activation than non-social pictures (see Table 2 and Fig. 1). Again, viewing emotional social pictures caused the most pronounced activation of the OFC (see Table 3).

#### 3.2. Brain activation during listening to emotional and social sounds

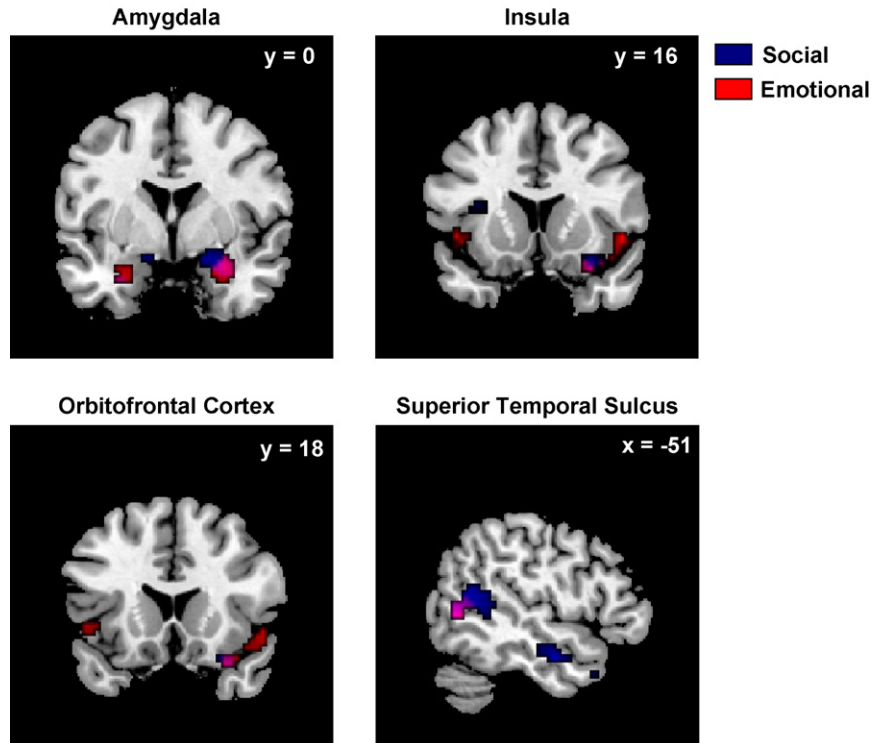
##### 3.2.1. Whole-brain-analysis

Listening to emotionally relevant sounds evoked stronger BOLD-signal strength than listening to neutral sounds in the superior temporal gyrus, the inferior frontal gyrus as well as in the posterior cingulate gyrus. Sounds with social contents evoked stronger activations than non-social sounds in various temporal and frontal brain areas as well as in the anterior cingulate gyrus. No brain region was more strongly activated by neutral than by emotional or by non-social compared to social sounds (see Tables 1 and 2 for an overview of main effects).

##### 3.2.2. Region-of-interest-analyses

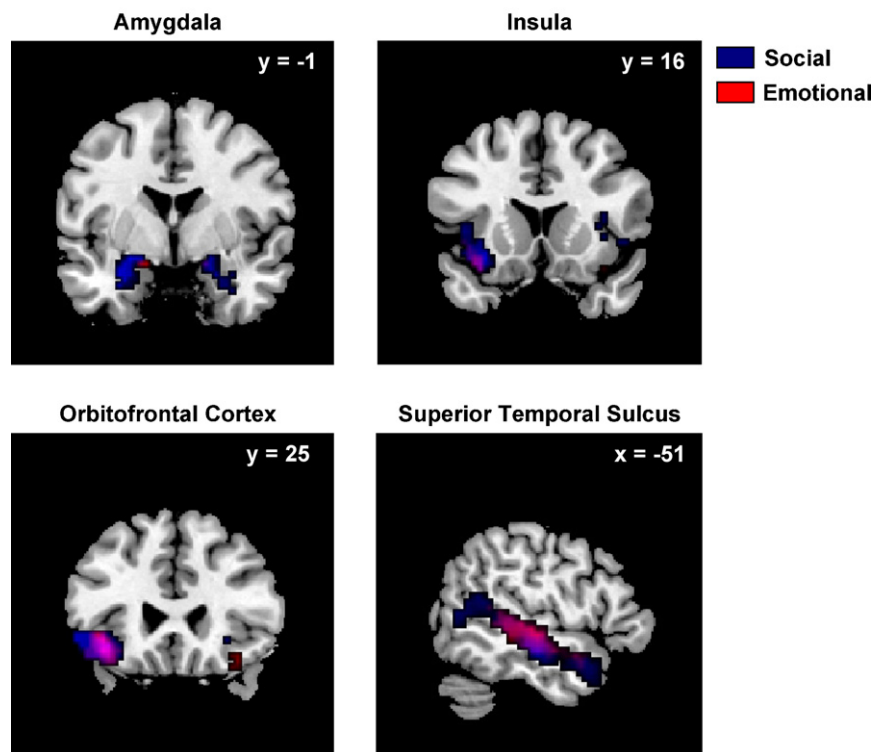
**3.2.2.1. Primary auditory cortex.** As expected, listening to emotional sounds evoked more pronounced bilateral activity in the primary auditory cortex than listening to neutral sounds (see Table 1 and Fig. 3). Moreover, listening to socially relevant sounds also resulted in stronger activity in the primary auditory

### ROI activation during viewing of emotional and social pictures



**Fig. 1.** Amygdala (upper left), anterior insula (upper right), superior temporal sulcus (STS, lower left), and orbitofrontal cortex (OFC, lower right) activation during visual emotional (red) and social (blue) stimulation superimposed on T1-images. For display purposes, activity was thresholded at  $p_{\text{uncorr.}} < 0.01$ .

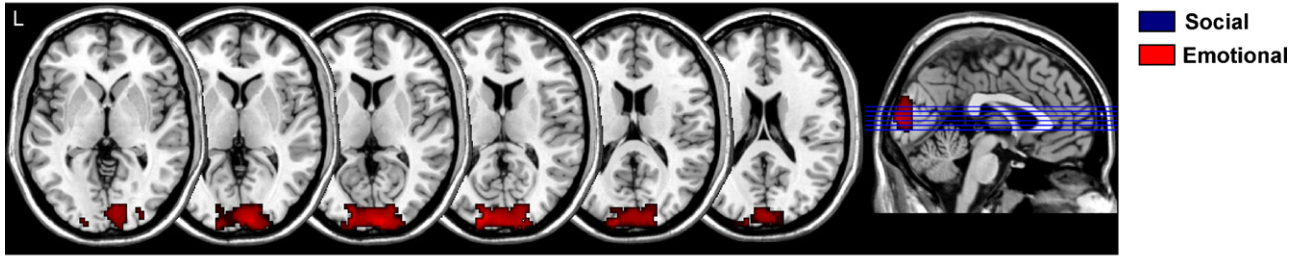
### ROI activation during listening to emotional and social sounds



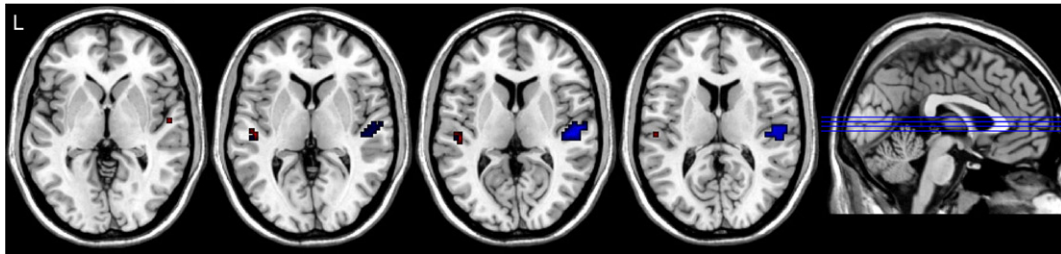
**Fig. 2.** Amygdala (upper left), anterior insula (upper right), superior temporal sulcus (STS, upper left), and orbitofrontal cortex (OFC, upper right) activation during auditory emotional (red) and social (blue) stimulation superimposed on T1-images. For display purposes, activity was thresholded at  $p_{\text{uncorr.}} < 0.01$ .

## Primary sensory cortex activation during perception of emotional and social stimuli

## Primary visual cortex activation



## Primary auditory cortex activation



**Fig. 3.** Primary visual (upper panel) and primary auditory cortex (lower panel) activation during perception of emotional (red) and social stimuli (blue) superimposed on T1-images. For display purposes, activity was thresholded at  $p_{\text{uncorr.}} < 0.01$ .

cortex than listening to non-social sounds (see Table 2 and Fig. 3). The interaction contrast revealed that emotional social sounds evoked the strongest bilateral activity in the primary auditory cortex (see Table 3).

**3.2.2.2. Amygdala.** Listening to emotional sounds elicited stronger BOLD-signal strength within the amygdala than listening to sounds with neutral contents (see Table 1 and Fig. 2). Listening to sounds with social contents also caused more pronounced amygdala activation than listening to sounds with non-social contents (see Table 2 and Fig. 2).

**3.2.2.3. Anterior insula.** Overall, listening to emotionally evocative sounds elicited significantly stronger left anterior insula activation than listening to neutral sounds (see Table 1 and Fig. 2). Furthermore, social auditory stimuli produced substantially stronger anterior insula activation than those with non-social contents (see Table 2 and Fig. 2). The interaction contrast revealed that listening to emotional social sounds caused the most pronounced bilateral insula activation (see Table 3).

**3.2.2.4. Superior temporal sulcus.** Listening to emotional sounds elicited more pronounced STS-activation than listening to neutral sounds (see Table 1 and Fig. 2). As expected, listening to sounds with social contents produced more STS-activation than listening to sounds with non-social content (see Table 2 and Fig. 2). Emotional sounds containing social content elicited the most pronounced bilateral STS-activation (see Table 3).

**3.2.2.5. Orbitofrontal cortex.** Listening to emotionally relevant sounds elicited more pronounced BOLD-responses in the OFC than listening to neutral sounds (see Table 1 and Fig. 2). Social auditory stimuli evoked more bilateral OFC activation than non-social sounds (see Table 2 and Fig. 2). As with the picture stimuli, listening to emotional social sounds elicited the most pronounced bilateral activations of the OFC (see Table 3).

#### 4. Discussion

The current study investigated brain activity evoked by visual and auditory emotional and neutral stimuli that either contained social information or not. Emotional compared to neutral stimuli evoked stronger bilateral activation in the amygdala, the anterior insula, the orbitofrontal cortex (OFC), and the superior temporal sulcus (STS). Importantly, stronger activation of this network was found during processing of both visual and auditory emotional compared to neutral stimuli. These findings indicate that these brain structures are important for processing the emotional relevance of the stimuli in the environment, irrespective of the sensory modality by which this emotional information is conveyed. Thus, auditory emotional stimuli elicited strong activation in the network described above extending previous findings of increased activation of the amygdala during processing of pleasant (vocalizations of laughter [31]) and unpleasant sounds (e.g. growling dog [4]). In the current experiment, the amygdala activation evoked by emotional sounds was much stronger than in the previous studies. One reason might be that half of the emotional sounds contained social information. Interestingly, encoding of socially relevant information from stimuli of the environment seems to engage the same network that is activated during processing of emotional contents irrespective of the sensory modality by which this information is conveyed.

Stronger bilateral activations for pictures depicting humans relative to non-human pictures (i.e., pictures depicting animals and objects) were found in the amygdala, the anterior insula, the OFC, and the STS. In the same vein, human sounds relative to non-human sounds elicited significantly stronger bilateral activation in the same areas of the brain. These data are in line with findings of stronger activation in the STS to vocal sounds than to non-vocal environmental sounds [5] as well as to anger prosody relative to neutral prosody [14]. Moreover, increased activation of amygdala during listening to human laughter has been reported [31]. Using single neuron recordings, increased responses to vocal sounds in the monkey amygdala were found [17]. Interestingly, 20% of all neurons in the amygdala responded to emotional expressions irrespective of whether they were conveyed by the visual (threatening facial expression) or by the auditory system (scream).

Independent of modality, emotional stimuli elicited more pronounced activation in the anterior insula, the superior temporal sulcus (STS), and the orbitofrontal cortex (OFC) when containing social information. In contrast, the amygdala showed pronounced main effects for emotional and social contents but an interactive effect only for visual stimuli in the right amygdala. Previously, similar interactive effects in the STS and additive effects in the amygdala have been reported [24]. However, most pronounced amygdala activation during social–emotional stimuli was also found [8]. The authors argued that the social dimension of emotion may be as neurobiologically distinct and meaningful as the valence dimension. Keltner and Kring emphasize the social function of emotion and proposed three general processes by which emotions shape social interactions, among them the idea that emotions serve as incentives for others' actions [16]. Thus, emotions elicited in social situations do not only help to organize one's own behavior but also structure interpersonal interactions. Therefore, social emotional stimuli may cause pronounced brain activations leading to distinct expressions and action tendencies which enable not only the person experiencing the own emotion but also other attendants to respond adaptively.

Replicating previous findings (see [28]), emotional pictures elicited significantly stronger activation in the primary visual cortex than neutral pictures. Additionally, it has been shown that the increased BOLD response in the primary visual cortex to emotional pictures is highly correlated with the activation in the amygdala [27]. According to the anatomical findings in monkeys [3], there are dense interconnections between the amygdala and the visual cortex suggesting that the network involved in the detection of stimulus significance are interacting with the primary sensory processing areas in the brain. Interestingly, in the current study, a similar result pattern was found in the primary auditory cortex. Both emotional and social sounds elicited more pronounced activity in the primary auditory cortex than their respective neutral control sounds. In contrast to the direct interconnections between amygdala and primary visual cortex, the information flow between the primary auditory cortex and the amygdala might be mediated by more rostral levels of the superior temporal cortex that has dense connections to both, the amygdala and the primary auditory cortex [3]. Our functional brain imaging data would support such connection because the left rostral superior temporal gyrus (BA 21) was extensively activated by emotional sounds.

#### 4.1. A dynamic processing model of significant stimuli

According to the *component process model of emotions* by Scherer, encoding of emotional events or stimuli can be organized into several sequential steps [32]. In this model, it is assumed that the first step in this sequential analysis is a so called relevance detection check in which the organism scans the environment for the occurrence of events requiring deployment of attention, further information processing, and possibly adaptive reaction. The brain imaging data of the current study suggests that a neural network centered around the amygdala is critically involved in this process of relevance detection. Increased amygdala activation is evident for stimuli that contain emotionally evocative and/or socially relevant information, irrespective in which sensory modality this information is conveyed. Interestingly, amygdala activation is even more pronounced if the emotional stimuli are difficult to detect [10] or presented very briefly [33]. These data suggest that the amygdala might indeed serve as a first step relevance detector [29]. According to the model, after the initial relevance detection, implications or consequences of a stimulus or event are evaluated. We found increased activation in the anterior insula and the OFC. While the insula is assumed to integrate information from the environment

with interoceptive information from the body [1,37], the OFC was described as a candidate structure for being involved in integrating the processing of the current stimulus with previous learning experiences [26]. Thus, although our brain imaging data do not allow assessing the temporal dynamics of the appraisal process the pattern of activation found in the current experiment would support the involvement of a neural network in the appraisal process that integrates cues from the environment and body sensations with previous learning experiences. We also found increased activation of the STS and the primary sensory cortices during processing of socially relevant and emotionally evocative stimuli suggesting that these relevant stimuli are tagged for more elaborate processing.

Taken together, the current findings support the idea that the amygdala, the insula, the STS, and the OFC work as a network that preferentially processes those stimuli from the environment that are relevant for the organism either due to their emotional impact or due to their relevance for social interaction. This network is engaged independently of the modality in which a relevant stimulus is presented. Future work should address the temporal characteristics of this network to identify feedback and feed-forward mechanisms involved in processing of relevant information.

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