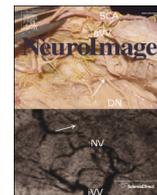


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The roles of superficial amygdala and auditory cortex in music-evoked fear and joy



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ABSTRACT

This study investigates neural correlates of music-evoked fear and joy with fMRI. Studies on neural correlates of music-evoked fear are scant, and there are only a few studies on neural correlates of joy in general. Eighteen individuals listened to excerpts of fear-evoking, joy-evoking, as well as neutral music and rated their own emotional state in terms of valence, arousal, fear, and joy. Results show that BOLD signal intensity increased during joy, and decreased during fear (compared to the neutral condition) in bilateral auditory cortex (AC) and bilateral superficial amygdala (SF). In the right primary somatosensory cortex (area 3b) BOLD signals increased during exposure to fear-evoking music. While emotion-specific activity in AC increased with increasing duration of each trial, SF responded phasically in the beginning of the stimulus, and then SF activity declined. Psychophysiological Interaction (PPI) analysis revealed extensive emotion-specific functional connectivity of AC with insula, cingulate cortex, as well as with visual, and parietal attentional structures. These findings show that the auditory cortex functions as a central hub of an affective-attentional network that is more extensive than previously believed. PPI analyses also showed functional connectivity of SF with AC during the joy condition, taken to reflect that SF is sensitive to social signals with positive valence. During fear music, SF showed functional connectivity with visual cortex and area 7 of the superior parietal lobule, taken to reflect increased visual alertness and an involuntary shift of attention during the perception of auditory signals of danger.

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Introduction

Of all emotions, fear is the one that has been investigated most intensely in affective neuroscience over the last decades. However, there is scarcity of functional neuroimaging studies on fear with music, and neural correlates of music-evoked fear have thus remained elusive. This stands in gross contrast to a long musical tradition of using musical means to evoke fear in the listener. The earliest theoretical treatise on such means is the Affektenlehre (“theory of affects”) of the Baroque, which prescribed musical methods and figures for imitating, or portraying (and thus, according to the Affektenlehre, summoning) emotions, including fear (Mattheson, 1739/1999). Among countless well-known examples of fear-evoking (Western) music are Handel's

Messiah (“And He Shall Purify”), Mozart's *Idomeneo*, the thunderstorm portrayed in Beethoven's sixth symphony, Berlioz' *Sonje d'une nuit du Sabbat*, Herrmann's music for *Psycho*, and Penderecki's *Polymorphia*.

Nevertheless, only two previous functional neuroimaging studies have investigated brain responses to fear-evoking music. One of these studies explored how fear music can enhance feelings of fear evoked by images (Baumgartner et al., 2006), but that study did not present fear music alone, thus leaving open the question as to which activation patterns would be evoked by fearful music alone (i.e., without negative visual images). The other study investigated how music evoking fear or joy can change the perception of neutral film clips (Eldar et al., 2007). The latter study also investigated brain responses evoked by the fear music alone (without film clips), compared to a baseline condition, in selected regions of interest (amygdala, anterior hippocampal formation, prefrontal cortex, and auditory cortex). However, no effects of fear music were observed without film-clips (nor effects of joy or neutral music without film-clips), neither in the amygdala, nor in the hippocampus or the prefrontal cortex. In addition, a study by Lerner et al.

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(2009) showed that listening to fear-evoking music with closed eyes (compared to listening with open eyes), evoked greater activation than open eyes in the amygdala/anterior hippocampal formation and anterior temporal poles (this effect of eyes open/closed was not observed when listening to neutral music). Main effects of fear compared to neutral music were not reported in that study. Finally, a recent study by *Trost et al. (2012)* reported brain activations due to music-evoked “tension” (characterized by feelings of high arousal and low valence), under which the authors also subsumed “feelings of anxiety and suspense induced by scary music” (brain activations included bilateral superior temporal gyrus, right parahippocampal gyrus, motor and premotor areas, cerebellum, right caudate nucleus, and precuneus). Notably, the concept of “tension” also includes emotional phenomena not related to fear, such as emotional reactions to unexpected musical events (*Huron, 2006*), and, therefore, *Trost et al. (2012)* argued that it is not clear whether the observed brain activations were due to fear responses, or to more general feelings of tension and unease. Thus, there are no functional neuroimaging data available that would allow us to draw conclusions about neural correlates of music-evoked fear.

With regard to lesion studies, *Gosselin et al. (2005)* showed impaired recognition of scary music in epileptic patients following unilateral medial temporal lobe excision (including the amygdala). In that study, both patients with left or right medial temporal lobe resections showed impaired recognition of scary, but not happy or sad, music. Corroborating this finding, data from a patient with bilateral damage restricted to the amygdala showed a selective impairment in the recognition of scary and sad music (*Gosselin et al., 2007*), indicating that the recognition of fear expressed by music involves the amygdala. These findings are reminiscent of findings reporting similar impairment for the recognition of fearful faces (reviewed in *Peretz, 2010*), suggesting that scary music and fearful faces are processed, at least in part, by common cerebral structures. Supporting this assumption, patients with unilateral anteromedial temporal lobe excision were found to be impaired in the recognition of both scary music and fearful faces (*Gosselin et al., 2011*), with results in both tasks being correlated. This suggested a multimodal representation of fear within the amygdala (although recognition of fearful faces was preserved in some patients, while their recognition of scary music was impaired). However, due to the size of the lesions in the reported studies, it remains unclear which nuclei of the amygdaloid complex played a role in the reported findings.

Functional neuroimaging studies on fear evoked by visual stimuli, recall/imagery, or auditory (but not musical) stimuli have also implicated the amygdaloid complex (*LeDoux, 2000*), in particular the basolateral amygdala (BL), as well as a range of functionally connected structures in fear responses (e.g., *Phan et al., 2002*). Such structures include the auditory cortex in auditory fear conditioning paradigms (*LeDoux, 2000*), as well as a large array of both cortical and subcortical structures, such as cingulate and insular cortex, hippocampus, parahippocampal cortex, orbitofrontal cortex, dorsolateral prefrontal cortex, striate (visual) cortex, basal ganglia, cerebellum, as well as brainstem regions such as the periaqueductal gray (*Roy et al., 2009; Stein et al., 2007; Williams et al., 2006*).

Based on the reported findings, we aimed to investigate the role of the amygdaloid complex and the auditory cortex, including their functional connections, for fear evoked by music. The cultural practice of using music to evoke fear makes music an important means to investigate neural circuits underlying fear (*Eerola and Vuoskoski, 2011*), in addition to the vast number of studies using visual stimuli to investigate neural correlates of fear. Besides fear stimuli, the present study also used joyful and neutral music. Joy was chosen as positive emotion because, on the one hand, both joy and fear are considered as “basic emotions” (*Ekman, 1999*), and both the expression of joy as well as of fear in Western music can be recognized universally (*Fritz et al., 2009*). On the other hand, other than, e.g. peaceful music (which is also perceived as positive, e.g. *Vieillard et al., 2008*), arousal levels evoked by joy music can well be matched with those evoked by fear

music. Similarly, musical and acoustical parameters such as tempo and pitch variation can well be matched between joy and fear music. Moreover, joyful music was chosen to replicate results of previous studies. Although only a few previous functional neuroimaging studies specifically used “happy” (*Brattico et al., 2011; Brown et al., 2004; Mitterschiffthaler et al., 2007*) or “joyful” (*Koelsch et al., 2006; Mueller et al., 2011*) music, these studies, along with other studies investigating musical frissons (*Blood and Zatorre, 2001; Salimpoor et al., 2011*), or music evoking emotional responses with positive valence and high arousal (*Trost et al., 2012*) indicate a number of relatively consistent features, namely stronger BOLD signal intensity (a) in the auditory cortex (*Brattico et al., 2011; Koelsch et al., 2006; Mitterschiffthaler et al., 2007; Mueller et al., 2011; Trost et al., 2012*), (b) the ventral striatum (*Blood and Zatorre, 2001; Brown et al., 2004; Koelsch et al., 2006; Menon and Levitin, 2005; Mitterschiffthaler et al., 2007; Trost et al., 2012*), (c) the anterior insula (*Blood and Zatorre, 2001; Brown et al., 2004; Koelsch et al., 2006*), and (d) the anterior cingulate cortex (*Blood and Zatorre, 2001; Janata, 2009; Mitterschiffthaler et al., 2007*). Moreover, (e) several studies on music-evoked emotions showed signal changes in the anterior hippocampal formation in response to stimuli with positive emotional valence (e.g., *Blood and Zatorre, 2001; Mueller et al., 2011; Trost et al., 2012*). Based on these findings, we hypothesized increased BOLD signals in response to joy stimuli (compared to neutral or fear stimuli) in the auditory cortex, ventral striatum, insula, ACC, and hippocampal formation.

Another aspect of our study was the investigation of the temporal dynamics of emotion across time. To our knowledge, only two previous functional neuroimaging studies have investigated the temporal dynamics of neural correlates of emotion (for habituation-effects across an experimental session see *Mutschler et al., 2010*). A study by *Salimpoor et al. (2011)* reported that BOLD signal intensity increased (a) in the dorsal striatum during the anticipation of a music-evoked frisson, and (b) in the ventral striatum during the experience of the frisson (notably, additional PET data showed that these signal increases were related to dopaminergic synaptic activity in these structures). Another study (*Koelsch et al., 2006*), in which stimuli of 60 s were split into two 30-second halves, showed that significant signal differences between pleasant and unpleasant music were most pronounced during the second half of the trials. The structures with such temporal dynamics of activation included the auditory cortex, inferior fronto-lateral areas (area 45 and the posterior part of the inferior frontal sulcus), anterior insula, the amygdaloid complex (probably basolateral amygdala), hippocampal formation, temporal poles, and parahippocampal cortex (a similar trend was observed in the ventral striatum).

Particular care was taken with regard to the acoustic parameters of our stimuli: numerous acoustical features of the stimuli were measured, which allowed us (1) to match joy, fear, and neutral stimuli with regard to numerous acoustical parameters (e.g., pitch variation, tempo, intensity, and spectral flux), and (2) to introduce acoustical factors that differed between conditions as regressors of no interest in the analysis of fMRI data. Provided that no crucial acoustical features were missed, this enabled us to investigate the role of the auditory cortex with regard to its emotion-specific interfacing with limbic/paralimbic structures. Previous work has implicated auditory association cortex (auditory parabelt), as well as its connections with the lateral amygdala, in fear conditioning (*LeDoux, 2000*). However, auditory parabelt regions project to numerous limbic/paralimbic structures (such as orbitofrontal cortex, insula, and cingulate cortex; e.g. *Petrides and Pandya, 1988; Smiley et al., 2007; Yuki, 1995*), and the role of these auditory projections for emotional processes, and thus the role that the auditory cortex plays for emotional processes, is largely unknown.

Summary of hypotheses

Motivated by the reported findings, we tested whether music-evoked fear, as compared to neutral or joy stimuli, would elicit signal changes in

the basolateral nucleus of the amygdaloid complex. For joy, as compared to neutral or fear, we expected stronger BOLD signal intensity in the ventral striatum, auditory cortex, hippocampal formation, insula, and cingulate cortex. Finally, to explore neural networks underlying joy and fear, we performed a Psychophysiological Interaction (PPI) analysis using the peak voxels indicated by the contrast analysis between conditions as seed voxels. More specifically, we were interested in emotion-specific functional connectivity between amygdaloid complex and auditory cortex, between auditory cortex and insula, as well as between auditory cortex and cingulate cortex.

Materials and methods

Participants

18 individuals (aged 20–31 years, $M = 23.78$, $SD = 3.54$, 9 females) took part in the experiment. All participants had normal hearing (as assessed with standard pure tone audiometry) and were right-handed (according to self-report). None of the participants was a professional musician, nor a music student. Seven participants had no formal musical training, eight participants had once received music lessons (mean duration of formal training was 2.81 years, $SD = 2.36$, instruments were: flute, drums, piano, violin, guitar and melodica) but had not played their instruments for several years ($M = 8.83$, $SD = 7.52$), and three participants had learned a musical instrument that they were still playing (mean duration of formal training was 12.5 years, $SD = 3.5$, instruments were: guitar, violin, piano and electric bass). Exclusion criteria were left-handedness, professional musicianship, past diagnosis of a neurological or psychiatric disorder, a score of ≥ 13 on Beck's Depression Inventory (BDI; Beck et al., 1993), excessive consumption of alcohol or caffeine during the 24 h prior to testing, and poor sleep during the previous night. All subjects gave written informed consent. The study was conducted according to the Declaration of Helsinki and approved by the ethics committee of the School of Life Sciences and the Psychology Department of the University of Sussex.

Stimuli and procedure

Musical stimuli were selected to evoke (a) feelings of joy, (b) feelings of fear, or (c) neither joy nor fear (henceforth referred to as neutral stimuli). There were $n = 8$ stimuli per category (the complete list of joy and fear stimuli is provided in Supplementary Table S1). Joy stimuli had been used in previous studies (e.g., Fritz et al., 2009; Koelsch et al., 2010a, 2011; Mueller et al., 2011) and consisted of CD-recorded pieces from various epochs and styles (classical music, Irish jigs, jazz, reggae, South American and Balkan music). Fear-evoking musical stimuli were excerpts from soundtracks of suspense movies and video games. To increase the fear-evoking effect of the fear stimuli, their relatively high acoustic roughness (see also next paragraph) was further increased: from each fear excerpt, two copies were obtained and pitch-shifted, one copy was shifted one semitone higher, the other copy a tritone lower (see also Fritz et al., 2009; Koelsch et al., 2006). Then, all three versions of one excerpt (original pitch, one semitone higher, and a tritone lower) were rendered as a single wav-file (pitch-shift and rendering was performed using Ableton Live, version 8.0.4, Ableton AG, Berlin, Germany). Neutral stimuli were sequences of isochronous tones, for which the pitch classes were randomly selected from a pentatonic scale. These tone sequences were generated using the MIDI (musical instrument digital interface) toolbox for Matlab (Eerola and Toiviainen, 2004). Importantly, for each joy–fear stimulus pair (see below), a neutral control stimulus was generated that matched joy and fear stimuli with regard to tempo, F0 range (i.e., range of the fundamental frequency), and instrumentation (using the two main instruments or instrument groups of the respective joy–fear pair). To create stimuli that sounded like musical compositions played with real instruments (similar to the joy and fear stimuli), the tones from the MIDI sequences were set to

trigger instrument samples from a high quality natural instrument library (X-Sample Chamber Ensemble, Winkler & Stahl GbR, Detmold, Germany) and from the Ableton Instrument library (Ableton AG, Berlin, Germany). Stimuli were then rendered as wav-files using Ableton Live. Using Praat (version 5.0.29; Boersma, 2002), all excerpts (joy, fear, and neutral) were edited so that they all had the same length (30 s), 1.5 s fade-in/fade-out ramps, and the same RMS power.

Importantly, joy and fear stimuli were chosen such that each joyful excerpt had a fearful counterpart that matched with regard to tempo (beats per minute), mean fundamental frequency, variation of fundamental frequency, pitch centroid value, spectral complexity, and spectral flux. This was confirmed by an acoustic analysis of the stimuli using 'Essentia', an in-house library for extracting audio and music features from audio files (<http://mtg.upf.edu/technologies/essentia>). The Essentia software was also used to specify acoustical differences between stimuli with regard to other acoustical factors: 177 acoustical descriptors were extracted frame-by-frame (frame length = 21.5 ms, 50% overlap), averaged along the entire duration of the file, and then compared between conditions (joy, neutral, fear) using one-way ANOVAs. Bonferroni-corrected significance-level was $0.05/177 = 0.00028$ (lowering this threshold for one-sided tests, i.e. 0.00056, did not change any of the results). The extracted features represent acoustic and musical features used in music information retrieval, i.e., different combinations of them are used for predictive models of musically relevant categorizations such as genre detection, instrument detection, key and mode detection, or emotional expression. Although these features have mostly been validated in machine-learning contexts (Huq et al., 2010; Kim et al., 2010; Laurier, 2011), it is possible that they also play a role for human auditory perception. In addition, many of the used parameters have been validated in perceptual experiments, such as features related to spectral complexity, F0, and F0 variations (Agrawal et al., 2012; Alluri et al., 2012; Coutinho and Dibben, 2012; Juslin and Laukka, 2003; Kumar et al., 2012), sensory dissonance (Coutinho and Dibben, 2012; Koelsch et al., 2006; Plomp and Levelt, 1965; Vassilakis and Kendall, 2010), spectral flux (Coutinho and Dibben, 2012; Menon et al., 2002), spectral centroid (Coutinho and Dibben, 2012), spectral crest (Laurier, 2011), temporal modulation frequencies (Kumar et al., 2012), key strength (Alluri et al., 2012; Krumhansl, 1990), and pulse clarity (Alluri et al., 2012). Significant effects of condition were indicated for the following acoustic factors (with F -values in parentheses, degrees of freedom: 2, 21): (a) Mean (72.3) and variance (13.8) of *F0 salience* (this measure is highest for single tones, intermediate for chords, and lowest for noises; note that mean F0 and variance of F0 did not differ between joy, fear, and neutral stimuli). The mean F0 salience was highest for neutral, intermediate for joy, and lowest for fear stimuli ($p < .0001$ in all pairwise comparisons). This reflects that both joy and fear (but not neutral) stimuli contained numerous harmonies, and that fear (but not joy) stimuli contained numerous percussive sounds, as well as hissing and whooshing noises. (b) Mean (41.3) and variance (28.0) of *sensory dissonance*. Sensory dissonance was lowest for neutral, intermediate for joy, and highest for fear stimuli. Mean sensory dissonance differed significantly between joy and neutral ($p < .0001$), between fear and neutral ($p < .0001$), and between joy and fear stimuli ($p < .05$). (c) Mean *chord strength* (25.2) and *key strength* (14.7); these factors measure how strongly a sound resembles the sound of a chord, and how clearly the sounds of a stimulus can be attributed to a key. Chord strength was higher for joy compared to fear stimuli ($p < .0001$), as well as for joy compared to neutral stimuli ($p < .0006$), whereas fear and neutral stimuli did not differ significantly from each other. Key strength was higher for joy compared to fear stimuli ($p < .0001$), and for neutral compared to fear stimuli ($p = .01$); joy and neutral stimuli did not differ significantly from each other ($p > .15$). (d) Mean (30.0) and variance (16.4) of *spectral flux* (a measure of spectral variation within sounds), mean (30.0) *spectral crest* (a measure of the inhomogeneity, or noisiness, of the spectrum) and mean (10.6) *spectral complexity* (which correlates with the amount of different timbres that are present

in a piece). Mean spectral flux, spectral crest, and spectral complexity were lowest for neutral stimuli (with significant differences between neutral and joy, as well as between neutral and fear stimuli, $p < .05$ in each test), and did not differ significantly between joy and fear stimuli ($p > .2$ in each test).

Prior to the MRI session, participants were presented with short (12 s) versions of each stimulus to obtain familiarity ratings: Participants rated their familiarity with each piece on a four-point scale (ranging from “To my knowledge I have never heard this piece before”, to “I know this piece, and I know who composed or performed it”). Participants were then trained on the rating procedure, using 12 s long excerpts of musical pieces that did not belong to the stimulus set used in the fMRI scanning session.

During the fMRI scanning session, stimuli were presented in a pseudo-random order so that no more than two stimuli of each stimulus category (joy, fear, neutral) followed each other. Participants were asked to listen to the musical stimuli with their eyes closed (see also Lerner et al., 2009). Each musical stimulus was followed by an interval of 2 s in which a beep tone of 350 Hz and 1 s duration signaled participants to open their eyes and to commence the rating procedure. During the rating procedure, participants indicated how they felt at the end of each excerpt with regard to valence (‘pleasantness’), ‘arousal’, ‘joy’ and ‘fear’. That is, participants provided ratings about how they felt, and not about which emotion each stimulus was supposed to express (Gabrielson and Juslin, 2003; Juslin and Västfjäll, 2008). Ratings were obtained with 6-point Likert scales (ranging from “not at all” to “very much”). The time interval for the rating procedure was 12 s and each rating period was followed by a 4 s rest period (during which participants closed their eyes again), amounting to a total length of 48 s per trial (see Fig. 1). The entire stimulus set was presented twice during the fMRI scanning session. Musical stimuli were presented using Presentation (version 13.0, Neurobehavioral systems, Albany, CA, USA) via MRI compatible headphones (under which participants wore earplugs). Instructions and rating screens were delivered through MRI compatible liquid crystal display goggles (Resonance Technology Inc., Northridge, CA,

USA) with integrated eye-tracker that allowed us to guarantee that participants opened and closed their eyes according to the instruction.

MR scanning

Scanning was performed with a 3 T Siemens Magnetom TrioTim. Prior to the functional MR measurements, a high-resolution ($1 \times 1 \times 1$ mm) T1-weighted anatomical reference image was acquired from each participant using a rapid acquisition gradient echo (MP-RAGE) sequence. Continuous Echo Planar Imaging (EPI) was used with a TE of 30 ms and a TR of 2000 ms. Slice-acquisition was interleaved within the TR interval. The matrix acquired was 64×64 voxels with a field of view of 192 mm, resulting in an in-plane resolution of 3 mm. Slice thickness was 3 mm with an interslice gap of 0.6 mm (37 slices, whole brain coverage). The acquisition window was tilted at an angle of 30° relative to the AC-PC line in order to minimize susceptibility artifacts in the orbitofrontal cortex (Deichmann et al., 2002, 2003; Weiskopf et al., 2007). Given the duration of our stimuli (30 s), a continuous scanning design was required to perform the PPI analysis (so that enough data points were available for meaningful correlation estimations, see below).

Data analysis

fMRI data were processed using LIPSIA 2.1 (Lohmann et al., 2001). Data were corrected for slicetime acquisition and normalized into MNI-space-registered images with isotropic voxels of 3 cubic millimeters. A temporal highpass filter with a cutoff frequency of 1/90 Hz was applied to remove low frequency drifts in the fMRI time series, and a spatial smoothing was performed using a 3D Gaussian kernel and a filter size of 6 mm FWHM.

A mixed effects block design GLM analysis was employed (Friston et al., 2007). Valence ratings, arousal ratings, familiarity ratings, psychoacoustic parameters that differed significantly between conditions (see Stimuli and procedure), and realignment parameters were included in the design matrix as covariates of no interest (Johnstone et al., 2006). Then, one-sample *t*-tests were calculated voxel-wise for the contrast between fear vs. joy, and corrected for multiple comparisons by the use of cluster-size and cluster-value thresholds obtained by Monte Carlo simulations with a significance level of $p < 0.05$ (Lohmann et al., 2008). The significant clusters identified in this analysis were used as regions of interest (ROIs) to compare the average signal intensity (averaged across all voxels in each cluster) within those clusters between fear and neutral, as well as between joy and neutral. In addition, to explore the temporal nature of the significant differences in activity between fear and joy, for each peak voxel of each significant cluster, the timecourse of activity was determined by computing the voxel intensity separately for each scan (i.e., with a temporal resolution of 2 s) and for each condition.

Temporal interaction analysis

To investigate possible interactions between emotion and time we split the data from each trial into first half (seconds 1 to 15) and second half (seconds 16 to 30), and calculated a statistical parametric map based on the interaction between emotion (two levels: joy, fear) and time (two levels: first half, second half). A first-level interaction contrast was calculated for each subject, and the contrast images were then used for voxel-wise one-sample *t*-tests at the second level (corrected for multiple comparisons by the use of cluster-size and cluster-value thresholds obtained by Monte Carlo simulations with a significance level of $p < .05$) to identify clusters of voxels for which the emotion \times time interaction was significantly different from zero.

PPI analysis

The timecourses of activity at the peak voxels identified in the contrast joy vs. fear, averaged together with the timecourses from adjacent voxels, were used as seeds for Psychophysiological Interaction

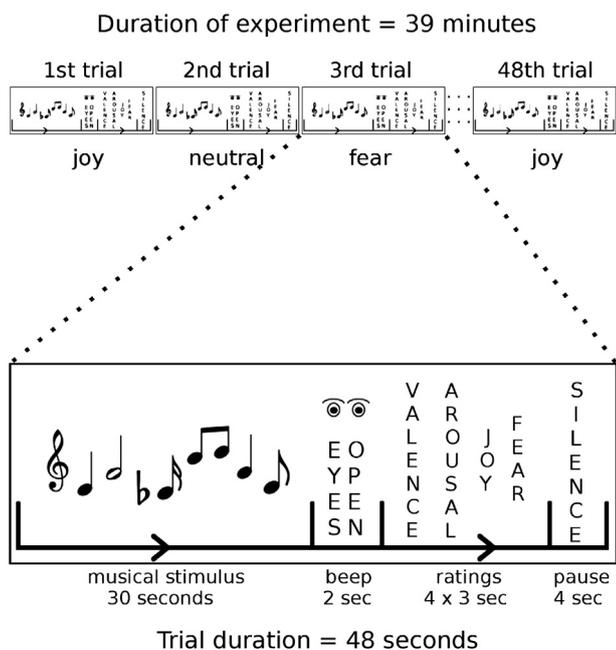


Fig. 1. Experimental design. In each trial, a music stimulus was presented for 30 s. Music stimuli were pseudorandomly either a joy, a fear, or a neutral stimulus. Participants listened to the music with their eyes closed. Then, a beep tone signaled to open the eyes and to commence the rating procedure. Four ratings (felt valence, arousal, joy, and fear) were obtained in 12 s, followed by a 4 s pause (during which participants closed their eyes again). Trial duration was 48 s, the experiment comprised of 48 trials.

(PPI) analyses to identify target regions for which the covariation of activity between seed and target regions was significantly different between experimental conditions. At the first level, contrasts were calculated for each subject based on the interaction term between emotion (joy vs. fear) and each seed voxel's timecourse of activity (Friston et al., 1997). For each seed voxel, the contrast images from all subjects were used in voxel-wise one-sample t -tests at the second level (corrected for multiple comparisons by the use of cluster-size and cluster-value thresholds obtained by Monte Carlo simulations with a significance level of $p < .05$) to identify clusters of voxels for which the psychophysiological interaction effect was significant.

Results

Behavioral data

Behavioral data are summarized in Fig. 2 and Table 1. Valence (pleasantness) ratings were lower for fear than for joy stimuli ($t(15) = 42.29, p < 0.0001$), higher for joy than for neutral stimuli ($t(15) = 16.10, p < 0.0001$), and did not differ significantly between neutral and fear stimuli ($t(15) = -1.94, p = .072$). Arousal ratings were higher for fear than for neutral stimuli ($t(15) = 11.84, p < 0.0001$), higher for joy than for neutral stimuli ($t(15) = 12.26, p < 0.0001$), and did not differ between joy and fear stimuli ($t(15) = .94, p = .36$). Joy ratings were lowest for fear stimuli, and highest for joy stimuli, with ratings for neutral stimuli being in between. Joy ratings differed significantly between fear and neutral stimuli ($t(15) = 9.03, p < 0.0001$), fear and joy stimuli ($t(15) = 32.32, p < 0.0001$), and between joy and neutral stimuli ($t(15) = 16.73, p < 0.0001$). Correspondingly, fear ratings were highest for fear stimuli, lowest for joy stimuli, with ratings for neutral stimuli

being in between. Although the degree of experienced fear was relatively moderate (4.02 on a scale from 1 to 6), fear ratings differed significantly between fear and neutral stimuli ($t(15) = 17.71, p < 0.0001$), fear and joy stimuli ($t(15) = 33.16, p < 0.0001$), and between joy and neutral stimuli ($t(15) = 9.93, p < 0.0001$). Average familiarity ratings were highest for joy stimuli, lowest for neutral stimuli, with ratings for fear stimuli being in between. Familiarity ratings differed significantly between joy and fear stimuli ($t(7) = 3.659, p < 0.05$), fear and neutral stimuli ($t(7) = 4.41, p < 0.01$), and between joy and neutral stimuli ($t(7) = 5.06, p < 0.0005$). Due to the differences in the behavioral ratings between stimulus categories with regard to valence, arousal, and familiarity, each participant's valence, arousal, and familiarity ratings were used in the fMRI data analysis as regressors of no interest (see Data analysis). Therefore, these variables (valence, arousal, and familiarity) did not contribute to the fMRI results presented in the following.

fMRI data

GLM analysis

The statistical parametric maps (SPMs) of the contrast *joy > fear* (corrected for multiple comparisons, $p < .05$) revealed significant BOLD signal differences in the auditory cortex (AC) bilaterally, and in the superficial amygdala (SF) bilaterally (see also Table 2 and Fig. 3a). The activation of the AC covered auditory core, belt, and parabelt regions bilaterally. The voxels with maximum z -values were located along Heschl's gyrus (HG), with the peak voxel in the left AC being located on the postero-lateral rim of HG (30% TE 1.2 according to Morosan et al., 2001), and the peak voxel in the right AC being located more medially on HG (90% TE 1.0 according to Morosan et al., 2001). In both left and right amygdala, the peak voxel was located in SF (left: 80% probability,

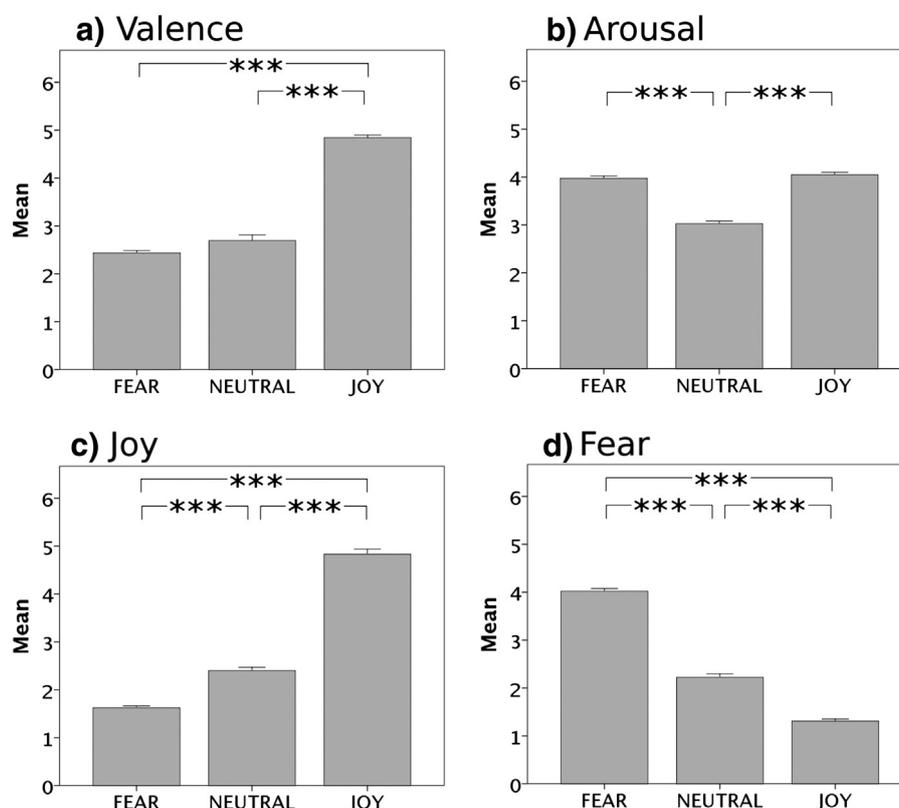


Fig. 2. Behavioral ratings of participants on the four emotion scales used in the present study: (a) valence, (b) arousal, (c) joy, and (d) fear. Range of scales was 1 to 6. Ratings are depicted separately for each stimulus category (fear, neutral, joy). Note that joy stimuli were rated as more pleasant than fear and neutral stimuli (valence/pleasantness ratings for fear and neutral stimuli did not differ from each other). Also note that arousal ratings of joy and fear stimuli did not differ from each other, and that both joy and fear stimuli were rated as more arousing than neutral stimuli.

Table 1

Descriptive statistics of behavioral data (mean, with standard deviation in parentheses). Range of valence, arousal, joy, and fear scales was 1 to 6, range of the familiarity scale was 1 to 4. For statistical tests see main text.

	Fear	Neutral	Joy
Valence	2.43 (0.20)	2.69 (0.48)	4.84 (0.21)
Arousal	3.97 (0.21)	3.03 (0.22)	4.05 (0.21)
Joyfulness	1.62 (0.16)	2.40 (0.29)	4.83 (0.42)
Fearfulness	4.02 (0.23)	2.22 (0.30)	1.31 (0.17)
Familiarity	1.44 (0.11)	1.17 (0.10)	2.01 (0.42)

right: 90% probability according to the cytoarchitectonic probability map by Amunts et al., 2005). The signal differences in SF extended bilaterally into the hippocampal-amygdaloid transition area (HATA, Amunts et al., 2005). The opposite contrast (*fear > joy*) showed signal differences in the anterior bank of the right postcentral gyrus (area 3b of the primary somatosensory cortex, S1, the peak voxel was located with 80% probability in this area according to Geyer et al., 1999). Contrasts with the neutral condition did not yield any additional activations (see also Table 2 and next section), except activations in the visual cortex for both *joy > neutral* (left V1, MNI-coordinate: -1, -82, -5; left V4: -33, -82, -14; right V2: 32, -99, 3) and *fear > neutral* (left V2, MNI-coordinate: -8, -95, 25; right V2: 23, -93, 26).

ROI analysis

To specify whether the observed differences between fear and joy were due to signal increase or decrease compared to the neutral control condition, ROI analyses were conducted for the significant clusters identified in the GLM analysis (AC, SF, S1), comparing the mean signal intensity of the voxels in each cluster between fear and neutral, as well as between joy and neutral. Results of these analyses (corrected for multiple comparisons, $p < .05$) showed that, compared to the neutral condition, there was stronger signal intensity during joy and weaker signal intensity during fear in the AC bilaterally as well as in the left SF (see also Table 2). In the right SF, signal intensity was weaker during fear compared to neutral (with no difference between joy and neutral). In the right S1, signal intensity was stronger during fear compared to neutral (joy and neutral did not differ from each other).

Timelines

To explore the temporal dynamics of the observed differences, the signal intensity of the peak voxel of each significant cluster (AC, SF, S1) was computed separately for each scan (i.e., with a temporal resolution of 2 s) in each condition. These timelines are shown in Fig. 4. In the AC, the auditory stimuli evoked a signal increase (in all conditions), with the signal intensity being generally highest for joy, lowest for fear, and intermediate for neutral (see next paragraph for statistical analysis). The most pronounced differences between conditions emerged at, and after around 10 s after stimulus onset. In SF, joy stimuli evoked a signal increase bilaterally, while fear stimuli evoked a signal increase only in the right SF. In the left SF, differences in signal intensity between fear and joy were particularly strong during the first half of the stimuli

(and a similar trend is observable in the right SF). Differences between conditions emerged several seconds after stimulus onset, were most pronounced at around 10 s, and vanished towards the end of the stimuli (see next paragraph for statistical analysis). In the right S1, all conditions evoked an initial signal decrease, followed by a signal increase (which was strongest for fear stimuli), and a decline of signal intensity towards the end of the stimuli.

Temporal interaction analysis

To statistically test the temporal dynamics observed in the timelines, and to further explore the temporal dynamics of differences between conditions in other structures (see Introduction), a temporal interaction analysis was computed with factors emotion (two levels: joy and fear) and time (two levels: first half and second half of each stimulus, see Materials and methods). Results (corrected for multiple comparisons, $p < .05$) are listed in Table 3 and summarized in Fig. 3b. Significant interactions were observed in the AC bilaterally, and in the left SF. This confirms the observations based on the timelines that differences in the AC were more pronounced during the second half, and in the SF during the first half of trials. Moreover, according to the hypotheses (see Introduction), significant emotion \times time interactions were observed bilaterally (a) in the posterior portion of the inferior frontal sulcus (IFS), (b) the anterior part of Broca's area (BA 45/46), and (c) in the ventral pallidum/ventral striatum (see also Fig. 3b). These interactions were due to more pronounced differences between conditions in the second compared to the first half. No interactions were observed in the hippocampus, parahippocampal gyrus, temporal poles, nor in the Rolandic operculum.

PPI analysis

Finally, we conducted a Psychophysiological Interaction (PPI) analysis (for details see Materials and methods). Seed regions were the peak voxels (as well as the directly adjacent voxels) identified in the GLM analysis in the direct contrast between fear and joy stimuli. Results of this analysis (corrected for multiple comparisons, $p < 0.05$), are listed in Table 4 and summarized in Fig. 3c.

Both left and right AC showed stronger functional connectivity during joy (compared to fear) with both ipsilateral and contralateral AC. In specific, the left posterior-lateral auditory belt showed stronger functional connectivity during joy with both left and right primary auditory cortex (left: 80%, right: 100% probability for TE 1.0 according to Morosan et al., 2001), as well as with lateral auditory belt-regions of both hemispheres. The right auditory core region showed stronger functional connectivity during joy with lateral auditory belt regions of both hemispheres (TE 2 according to Morosan et al., 2001, no probabilistic maps are available for this region). During fear (compared to joy), both left and right AC showed stronger functional connectivity with the cuneus (areas 17 and 18), the median wall of the precuneus (areas 5 and 7), and almost the entire cingulate sulcus (CS), from the pre-genua CS to the ascending branch of the (posterior) CS. Moreover, both left and right AC showed stronger functional connectivity during fear with the anterior insula bilaterally, and the left (but not

Table 2

Results of General Linear Model (GLM) contrasts, corrected for multiple comparisons ($p < .05$): (a) *joy > fear*, (b) *fear > joy*. The two outermost right columns provide the p -values for comparisons involving the neutral condition within the significant clusters identified in the GLM analysis (region of interest analysis). The diamonds in the outermost right column indicate that differences between fear and neutral were due to higher signal intensity during neutral than during fear. Abbreviations: ROI: region of interest; l: left; r: right; n.s.: not significant.

	MNI coordinate	Cluster size (mm ³)	z-Value: max (mean)	p-Value ROI: joy vs. neutral	p-Value ROI: fear vs. neutral
(a) <i>joy > fear</i>					
l Heschl's gyrus	-56 -14 7	16,038	6.36 (3.76)	.0002	.0001 \diamond
r Heschl's gyrus	50 -16 8	13,176	5.55 (3.72)	.0006	.0007 \diamond
l superficial amygdala	-17 -7 -15	486	4.32 (3.36)	.02	.009 \diamond
r superficial amygdala	22 -6 -13	324	3.40 (3.09)	n.s.	.03 \diamond
(b) <i>fear > joy</i>					
r postcentral gyrus (area 3b)	52 -13 36	297	-3.50 (-3.11)	n.s.	.0001

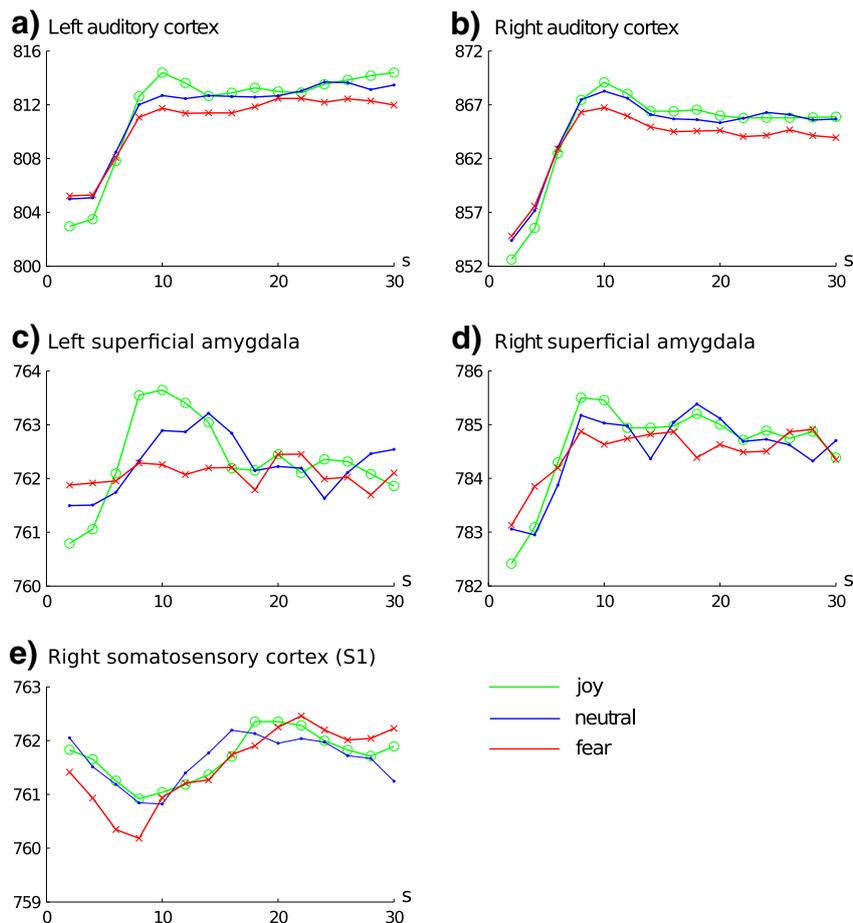


Fig. 4. Timelines depicting average BOLD signal intensity in the regions that significantly differed in the GLM contrast joy vs. fear. The ordinate represents values of voxel intensity, the abscissa represents time (in seconds), zero corresponds to the onset of trials.

neutral in between. A similar pattern was observed for the superficial amygdala (SF), except that joy vs. neutral did not differ from each other in the right SF. In S1, fear evoked stronger BOLD signals than both neutral and joy (joy vs. neutral did not differ). In AC bilaterally, responses were stronger during the second half of each trial (and the same phenomenon was observed in area 45, the IFS, and the ventral pallidum/ventral striatum). By contrast, BOLD signals in the left SF were stronger during the first half. PPI results showed that both left and right AC showed stronger functional connectivity during joy

(compared to fear) with both the ipsilateral and the contralateral AC. During fear (compared to joy), both left and right AC showed stronger functional connectivity with the cuneus (areas 17 and 18), the median wall of the precuneus (areas 5 and 7), and almost the entire cingulate sulcus (CS). Moreover, both left and right AC showed stronger functional connectivity during fear with the anterior insula bilaterally, and the left (but not the right) AC showed stronger functional connectivity during fear with areas 3a & b of S1. The left SF showed stronger functional connectivity during joy (compared to fear) with right posterior Heschl's gyrus. During fear (compared to joy), the left SF showed stronger functional connectivity with cuneus (V1–V4), and area 7a of the superior parietal lobule (precuneus) bilaterally. The right SF showed stronger functional connectivity during joy (compared to fear) with the mediodorsal nucleus of the thalamus.

Table 3
Results of the interaction contrast of emotion (joy vs. fear) × time (1st half vs. 2nd half of each trial), corrected for multiple comparisons ($p < .05$). Abbreviations: AC: auditory cortex; FOp: frontal operculum; SF: superficial amygdala; STG: superior temporal gyrus; l: left; r: right.

	MNI coordinate	Cluster size (mm ³)	z-Value: max (mean)
l post. IFS	−51 18 31	1809	4.02 (3.39)
r post. IFS	45 21 34	1134	3.76 (3.17)
l pars triangularis (area 45) ^a	−51 30 10	–	3.76 (–)
r pars triangularis (area 45)	51 30 10	513	3.27 (3.26)
l ant insula/deep FOp	−34 34 4	621	4.22 (3.27)
l ant. STG	−60 −9 −2	1377	4.56 (3.45)
r ant. STG/planum polare	51 0 −8	2214	4.81 (3.40)
l planum temp. (AC)	−42 −30 13	2457	3.94 (3.35)
r planum temp. (AC)	45 −27 19	5589	4.50 (3.42)
l SF	−21 −6 −14	324	3.51 (3.19)
l pallidum	−15 0 7	1296	4.42 (3.47)
r pallidum	11 3 4	378	3.79 (3.31)

^a The peak voxel in the l pars triangularis was part of the cluster with the maximum peak voxel in the l insula/deep frontal FOp.

Auditory cortex and emotional processing

Pronounced emotion-specific effects were observed in the auditory cortex: In the General Linear Model (GLM) contrast, BOLD responses in the entire supratemporal cortex (auditory core, belt, and parabelt) were stronger for joy than neutral stimuli, and stronger for neutral than fear stimuli. As will be argued in the following, these results indicate a prominent role of the auditory cortex in the emotional processing of auditory information. Importantly, there are five reasons as to why the activity differences between conditions cannot simply be due to acoustical factors: (1) the values of acoustical descriptors that significantly differed between conditions were included as covariates of no interest, and should therefore not have contributed to differences between conditions observed in the GLM contrasts. (2) However, even if

Table 4

Results of PPI analysis (corrected for multiple comparisons, $p < .05$), separately for the seed voxels in: (a) left AC (Heschl's gyrus), (b) right AC (Heschl's gyrus), (c) left SF, and (d) right SF (the PPI analysis with S1 as seed region did not indicate any results). Positive z -values (outermost right column) indicate stronger functional connectivity during joy compared to fear, whereas negative z -values indicate stronger functional connectivity during fear compared to joy. Abbreviations: AC: auditory cortex; FOp: frontal operculum; HG: Heschl's gyrus; ITS: inferior temporal sulcus; MD: mediodorsal; MTG: middle temporal gyrus; PAC: primary auditory cortex; SF: superficial amygdala; SFS: superior frontal sulcus; SPL: superior parietal lobule; STG: superior temporal gyrus; l: left; r: right.

	MNI coordinate	Cluster size (mm ³)	z -Value: max (mean)
(a) Left auditory cortex			
l HG (PAC)	51 – 18 7	2349	4.26 (3.17)
r HG (PAC)	–51 – 18 7	1431	3.77 (3.16)
r supramarginal gyrus	63 – 24 34	89,235	–4.97 (–3.22)
cuneus (area 17, 18)	9 – 66 4	19,764	–3.99 (–3.07)
l post. MTG/ITS	–60 – 60 7	2646	–4.19 (–3.17)
l anterior insula	–42 9 1	7263	–4.52 (–3.16)
l mid-insula ^a	–41 – 5 14	–	–3.5 (–)
l post. insula ^b	–36 – 20 11	–	–3.68 (–)
(b) Right auditory cortex			
l SFS	–24 30 52	2997	–4.07 (–3.19)
l SFS	–24 51 25	756	–3.92 (–3.04)
r SFS	27 42 37	3672	–3.76 (–3.05)
l ant. insula/deep FOp	–45 12 1	648	–4.06 (–3.27)
l mid-insula	–34 3 16	459	–3.48 (–3.05)
r ant. insula & putamen	27 12 7	2295	–4.35 (–3.17)
l planum temporale	–60 – 24 7	2970	4.34 (3.22)
r planum temporale	60 – 18 4	1188	3.68 (3.13)
r supramarginal gyrus	63 – 42 37	3429	–4.65 (–3.17)
l post. MTG/ITS	–60 – 66 7	3240	–4.40 (–3.24)
r post. MTG	54 – 57 13	5427	–3.81 (–3.06)
pre-genua cingulate	–6 42 7	2268	–3.64 (–2.98)
cingulate sulcus	3 15 43	3888	–4.38 (–3.13)
post. cingulate sulcus	6 – 30 49	33,264	–5.40 (–3.18)
(c) Left superficial amygdala			
r planum temporale/post. HG	42 – 33 13	567	3.75 (3.05)
r SPL (area 7)	18 – 48 54	351	–4.13 (–2.94)
l SPL (area 7)	–21 – 51 54	756	–4.56 (–3.21)
r sup. occipital gyrus (area 18)	26 – 95 20	7020	–3.68 (–2.87)
l middle occipital gyrus	–30 – 78 19	11,043	–4.24 (–2.99)
l lingual gyrus (V4)	–18 – 73 – 5	675	–2.94 (–2.69)
r lingual gyrus (V3 & V4)	18 – 81 – 8	648	–2.85 (–2.67)
(d) Right superficial amygdala			
MD thalamus	3 – 12 4	297	3.22 (2.93)

^a The peak voxel in the l mid-insula was part of the cluster with the maximum peak voxel in the l ant. insula.

^b The peak voxel in the l post.-insula was part of the cluster with the maximum peak voxel in the l ant. insula.

this procedure did not cancel out acoustical differences between conditions, joy and fear stimuli did not differ with regard to their intensity, mean F0 frequency, variation of F0 frequency, pitch centroid value, spectral complexity, and spectral flux. (3) F0 salience and chord strength differed significantly between joy and fear stimuli, as well as between joy and neutral stimuli (F0 salience was highest for neutral, intermediate for joy, and lowest for fear stimuli; chord strength was highest for joy stimuli, and did not differ between neutral and fear stimuli). Nevertheless, in the GLM, BOLD signal intensity in the auditory cortex was stronger in response to joy compared to neutral, and during neutral compared to fear stimuli; this pattern does not correlate with the pattern of F0 salience (being strongest for neutral stimuli) or the pattern of chord strength (which did not differ between neutral and fear stimuli). (4) Key-strength showed differences between joy and fear, as well as between fear and neutral stimuli, but not between joy and neutral stimuli. Again, this pattern is not consistent with the pattern of BOLD responses observed in the auditory cortex. Although not well known, it is highly likely that extraction of the key of tonal music (including extraction of a tonal center) involves both posterior and anterior supratemporal cortex bilaterally (e.g., Koelsch, 2011; Liegeois-Chauvel et al., 1998; Patterson et al., 2002; Peretz and Zatorre, 2005). Therefore,

the interactions of the auditory cortex with limbic/paralimbic brain structures are likely to be due to emotional processes, rather than being merely due to cognitive processes related to the key-strength of sounds. (5) Although fear stimuli had a higher degree of sensory dissonance than joy stimuli, activity changes in the auditory cortex are unlikely to be due to this difference only, because neutral stimuli were even more consonant than joy stimuli. The pattern of BOLD signal intensity observed in the GLM contrast is, thus, not related to the degree of sensory dissonance of the stimuli.

Instead, the observed pattern of BOLD signal intensity in the AC corresponds to the emotion ratings for joy (and inversely for fear, respectively), indicating that activity of the auditory cortex is related to the emotional quality of auditory information: Compared to neutral, BOLD signals had a higher intensity during the joy condition, and a lower intensity during the fear condition. In other words, we observed an actual increase in BOLD activity during listening to joy stimuli and an actual decrease during listening to fear stimuli (compared to neutral stimuli). With regard to the pronounced regional activity in the auditory cortex during the joy-evoking music (as indicated by the GLMs), it is likely that this was in part due to a more detailed acoustical analysis of the joyful music, which was probably related to a voluntary shift of attention: participants had a preference for the joy stimuli (as indicated by the valence ratings), and therefore probably paid more voluntary attention to those stimuli, leading to a stronger auditory cortex activation (Jäncke et al., 1999). Similar findings have previously been reported for pleasant compared to unpleasant music (Koelsch et al., 2006; Mueller et al., 2011) or pleasant vs. unpleasant sounds from the International Affective Digitized Sound System (IADS, Plichta et al., 2011). However, it is unlikely that merely preference (and, correspondingly, voluntary shifts of attention) explains this effect, because the preference of participants was comparable between fear and neutral music (again, as indicated by the valence ratings), and yet BOLD signal intensity differed between fear and neutral.

The role of the auditory cortex in the emotional processing of auditory information is further highlighted by the PPI results involving auditory seed regions: These results revealed emotion-specific functional connectivity (a) between auditory cortical areas and cingulate, as well as insular cortex during joy stimuli, and (b) between auditory areas and parietal, as well as visual cortex (V1–V5) during fear stimuli. Both cingulate and insular cortex are involved in emotional processes, in particular with regard to autonomic regulation as well as the production of subjective feelings (Craig, 2009; Medford and Critchley, 2010). In addition, the cingulate cortex has been implicated in the coordination of autonomic activity, behavior, motor expression, as well as cognitive processes in response to emotionally salient stimuli (Koelsch et al., 2010b; Medford and Critchley, 2010).

With regard to the marked functional connectivity between auditory areas and parietal as well as visual cortex, anatomical studies indicate that core, belt and parabelt regions project to V1 and V2 of visual cortex, and that neurons in V2 project back into these auditory regions (reviewed in Smiley et al., 2007). The observed functional connectivity between these areas in the present study highlights the role of auditory–visual interactions, in particular during emotional states of fear. The functional significance of such interactions is probably increased visual alertness in the face of danger signaled by auditory information (probably including involuntary shifts of attention). Our results are the first to show that the auditory cortex is a central hub of an affective-attentional network that is more extensive than previously believed, involving functional connectivity of auditory association cortex with a diverse range of visual, attentional, and limbic/paralimbic structures. This finding also supports the notion that multisensory interactions in the cerebral cortex are not limited to established polysensory regions, but that “interactions with other sensory systems also take place in auditory cortex” (Smiley et al., 2007). Notably, this latter conclusion holds even if such multisensory interactions were due to acoustical features which were possibly not accounted for by the

computational feature extraction (and not necessarily related to emotional responses).

Many of the observed emotion-specific functional connections parallel anatomical connections previously described in monkeys (as described below). Our results provide information about the emotion-specific nature of such connections. With regard to functional connections to the insula, our results parallel connections between posterior AC and neighboring granular insula in macaque monkeys (Smiley et al., 2007), taken as a likely source of somatosensory input into the AC (Smiley et al., 2007). In addition, we observed functional connectivity not only with posterior, but also with mid- and anterior insula. This indicates clear functional connectivity between AC and the insula in humans, possibly reflecting sensory-limbic interactions that are more pronounced in humans than in monkeys. Such sensory-limbic interactions are also apparent in the extensive functional connectivity between AC and cingulate cortex. Previous studies with monkeys showed anatomical connections between (lateral) auditory belt and posterior cingulate cortex (Yukie, 1995). Our data suggest more extensive functional connections between auditory cortex and cingulate cortex in humans that also include anterior cingulate regions.

Superficial amygdala and its role for joy and fear

The superficial amygdala (SF) showed higher BOLD signal values bilaterally during joy compared to the fear stimuli. These findings corroborate previous reports of (right) SF activation in response to pleasant joyful music (compared to unpleasant music-like noise, Mueller et al., 2011). Due to its dense anatomical connections to the ventral striatum (from which it evolved phylogenetically, Nieuwenhuys et al., 2008), the superior amygdaloid complex has so far been implicated in positive emotion and hedonic processes (Nieuwenhuys et al., 2008), in line with our results. In addition, the superior amygdaloid complex has reciprocal connections to the orbitofrontal cortex (Bach et al., 2011) and plays a role for olfactory processes (Heimer and Van Hoesen, 2006; Price, 2003). Further functional connections include the caudate, cingulate cortex, insula, and hippocampus (Roy et al., 2009). Interestingly, a study by Goossens et al. (2009) suggested that the SF is particularly sensitive to social stimuli. Thus, in the present study, the joyful music possibly evoked activity within the SF due to the extraction of the social significance of the joyful music (but see also below). Such significance emerges from several social functions of music, including communication, coordination of movements, cooperation, and social cohesion (summarized in Koelsch, 2010). The fear stimuli, on the other hand, had no socially incentive value (being a signal of threat, and thus motivating withdrawal), probably resulting in decreased neuronal activity within the SF bilaterally (compared to joy and neutral stimuli). The fact that fear stimuli evoked significantly weaker responses in the right SF compared to a neutral control condition, and virtually no signal change in the left SF, suggests that the pattern of SF response to an auditory signal codes the emotional quality of that stimulus (i.e., whether the stimulus is an incentive social signal, or a signal of threat). Note that it is unlikely that SF simply codes valence (or arousal), for two reasons: *first*, to our knowledge, no previous study using stimuli that are perceived as rewarding, but do not have a social component (such as monetary rewards) reported SF activation, and *second*, valence as well as arousal ratings were used as regressors of no interest in the statistical modeling of the data, and are thus unlikely to contribute to the present fMRI results.

The PPI results reveal that functional connectivity between (left) SF and auditory regions was stronger during joy than during fear stimuli. Although previous studies have shown anatomical and functional connections between the basolateral (BL) amygdala and AC that are involved in fear conditioning (LeDoux, 2000), the significance of functional connectivity of the SF has remained elusive. As argued above, such connectivity is perhaps related to the social significance of stimuli, in contrast to the connectivity between BL and AC, which

appears to be important for the conditioning of (auditory) signals of danger. It has recently been proposed (Kumar et al., 2012) that amygdala activity affects AC activity as a function of the emotional valence of stimuli (and that AC provides limbic/paralimbic structures with information about the acoustic quality of sounds). Thus, the functional connectivity between (left) SF and AC observed in the present study is in part consistent with the results by Kumar et al. (2012), because the stronger AC activity during joy (compared to fear) might be related to amygdalar activity (note that the functional connectivity between SF and AC was stronger during joy than fear, and that joy also evoked stronger BOLD signals than fear in AC). The neural pathway that originates in SF and modulates AC activity remains to be specified; as will be discussed below, such a pathway probably involves thalamic nuclei, including the medio-dorsal thalamus. Notably, the study by Kumar et al. (2012) presented unpleasant stimuli only, thus our results suggest that amygdala activity is also related to AC activity in response to pleasant auditory stimuli.

In addition to joy, SF is also involved in fear responses, as indicated by the increased functional connectivity of the (left) SF with area 7 and with visual areas during fear (compared to joy), possibly related to the elicitation of increased visual alertness during fear-evoking auditory information. Finally, the right SF showed increased functional connectivity during joy with the medio-dorsal thalamus (MD). A diffusion-tensor-imaging study by Behrens et al. (2003) reported a fiber tract extending anteriorly and inferiorly along the medial wall of the thalamus, then turning laterally into the amygdala. A similar path has been documented for non-human primates, via the inferior thalamic peduncle (Aggleton and Mishkin, 1984). In the study by Behrens et al. (2003), this pathway was small, and the authors were thus not confident that their result was valid. However, our results suggest that this pathway from MD to the (superficial) amygdala exists, and that it plays a specific role for positive emotion. Perhaps this thalamic nucleus is part of the pathway by which AC activity is regulated as an effect of SF activity.

Contrary to our hypothesis, no activity changes were observed between conditions in the hippocampal formation. However, the activity changes observed in the SF spread into the hippocampal-amygdaloid transition area, and perhaps stronger signal changes in the hippocampal formation would have been obtained in a less noisy environment: Mueller et al. (2011) reported that significant signal changes in the hippocampal formation (evoked by pleasant joyful music contrasted to unpleasant music-like noise) were observed only with interleaved silent steady state scanning, or with sparse temporal scanning; no signal change was observed in the hippocampus during continuous scanning in that study.

Primary somatosensory cortex (S1)

Stronger BOLD signals were measured in right area 3b of S1 during fear than during joy (or neutral) in voxels that correspond to the cortical representation of the face in S1 (Blakemore et al., 2005; Moulton et al., 2009). Previous experiments have reported that the recognition of emotions from visually presented facial expressions requires right somatosensory-related cortices, including the face representation in S1 (Adolphs et al., 2000). That finding corroborated the notion that individuals recognize another individual's emotional state by internally generating somatosensory representations that simulate how the other individual would feel when displaying a certain emotional (facial) expression. Our data suggest that such somatosensory-driven simulations are also activated by auditory information with emotional valence, such as music (probably also affective prosody). This notion is consistent with data indicating facial mimicry in response to happiness or sadness expressed by music (Lundqvist et al., 2009). It is also possible that somatosensory activity reflects mapping of an evoked emotional state during the emergence of feelings with the aid of somatosensory representations (e.g., of proprioceptive information during

visually evoked emotions, Rudrauf et al., 2009). Again, our results suggest that such mapping can be activated by auditory information with emotional valence. The reason as to why, in our study, S1 representations were activated more strongly in response to fear than to joy remains to be specified.

Conclusions

This study has two main conclusions: First, during music listening, the auditory cortex has emotion-specific functional interactions with a diverse range of visual, parietal, and limbic/paralimbic structures; this demonstrates that the auditory cortex is a central relay of an affective-attentional network that is more extensive than previously believed. This finding also implicates that the auditory cortex is involved in sensory-limbic and multisensory interactions that resemble those of established polysensory regions. Second, our results suggest that the superficial amygdala (SF) is sensitive for incentive social signals (including music), but at the same time also involved in fear responses: in concert with the auditory cortex, the SF appears to elicit increased visual alertness in the face of danger signaled by auditory information. Fear music may thus activate phylogenetically old mechanisms that engage the visual localization of potentially threatening objects. It is tempting to speculate that the corresponding increase of activity in visual areas during listening to fear-evoking music leads to more intense visual imagery (compared, e.g., to joyful music), particularly when listening to music with closed eyes (as in the present study). Such increased visual imagery during fear-evoking music might be an important factor contributing to the emotional experience, and the esthetic appeal, of fear-evoking music.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2013.05.008>.

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Conflict of interest

The authors declare that they do not have any conflict of interest.

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