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Author(s): Bogert, Brigitte; Numminen-Kontti, Taru; Gold, Benjamin; Sams, Mikko; Numminen, Jussi; Burunat, Iballa; Lampinen, Jouko; Brattico, Elvira

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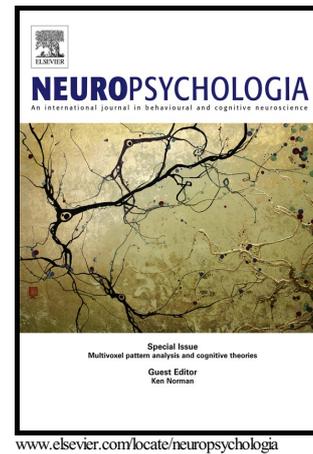
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Hidden sources of joy, fear, and sadness: Explicit versus implicit neural processing of musical emotions

Bogert, Brigitte^{1,2*}, Numminen-Kontti, Taru¹, Gold, Benjamin^{1,2}, Sams, Mikko³, Numminen, Jussi⁴, Burunat, Iballa⁵, Lampinen, Jouko³, Brattico, Elvira^{1,6,7*}

¹Cognitive Brain Research Unit (CBRU), Institute of Behavioural Sciences, University of Helsinki, Finland

²Montreal Neurological Institute, McGill University, Montreal, Canada

³Brain and Mind Laboratory, Department of Biomedical Engineering and Computational Science (BECS), School of Science, Aalto University, Espoo, Finland

⁴Helsinki Medical Imaging Center, University of Helsinki, Töölö Hospital, Finland

⁵Finnish Center for Interdisciplinary Music Research, Department of Music, University of Jyväskylä, Finland

⁶Center for Music in the Brain (MIB), Department of Clinical Medicine, Aarhus University & The Royal Academy of Music Aarhus/Aalborg, Aarhus, Denmark

⁷AMI Centre, Aalto University, Espoo, Finland

* **Address for correspondence:** Prof. Elvira Brattico. Center for Music in the Brain (MIB). Department of Clinical Medicine. Nørrebrogade 44, Building 10G. 8000 Aarhus C, DENMARK. Telephone: +45-78463030; E-mail: elvira.brattico@clin.au.dk

Abstract

Music is often used to regulate emotions and mood. Typically, music conveys and induces emotions even when one does not attend to them. Studies on the neural substrates of musical emotions have, however, only examined brain activity when subjects have focused on the emotional content of the music. Here we address with functional magnetic resonance imaging (fMRI) the neural processing of happy, sad, and fearful music with a paradigm in which 56 subjects were instructed to either classify the emotions (explicit condition) or pay attention to the number of instruments playing (implicit condition) in 4-sec music clips. In the implicit vs.

explicit condition, stimuli activated bilaterally the inferior parietal lobule, premotor cortex, caudate, and ventromedial frontal areas. The cortical dorsomedial prefrontal and occipital areas activated during explicit processing were those previously shown to be associated with the cognitive processing of music and emotion recognition and regulation. Moreover, happiness in music was associated with activity in the bilateral auditory cortex, left parahippocampal gyrus, and supplementary motor area, whereas the negative emotions of sadness and fear corresponded with activation of the left anterior cingulate and middle frontal gyrus and down-regulation of the orbitofrontal cortex. Our study demonstrates for the first time in healthy subjects the neural underpinnings of the implicit processing of brief musical emotions, particularly in frontoparietal, dorsolateral prefrontal, and striatal areas of the brain.

Keywords: music; emotion; implicit processing; explicit processing; caudate

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1. Introduction

Music is an important tool for the induction and regulation of emotion (North et al., 2004; Sloboda et al., 2001). However, this induction and regulation typically occurs when music is playing in the background and one is occupied with another primary activity. In one study, about 76% of participants reported music listening as an accompaniment to their primary activity (Lonsdale & North, 2011). The presence and type of music played in the background during purchasing can affect consumer behavior without the consumers' awareness of it (Milliman, 1982, 1986). Several behavioral tests have corroborated the subliminal effects of music on the general mood state (distinct from an emotion for its lower intensity and longer duration) of a subject and even on the perception of emotions conveyed through another sensory modality. For instance, music-induced elevated or depressed mood affected subjects' explicit evaluation of emotional faces: during depressing music subjects detected more rejection and fear (Bouhuys et al., 1995). Similarly, music may affect subjects' subconscious perception of visual emotions: in a gender discrimination task subjects reacted more quickly to happy faces in the presence of relaxing music than angry faces while listening to an irritating noise, evidencing a combination of a congruence bias for positive music-induced mood toward positive emotions and an attention shift away from the stimuli by the negative noise-induced mood (Quarto et al., 2014).

Further compelling evidence of implicit musical effects comes from studies of brain-damaged patients suggesting that cortical processing may not be essential for music to arouse emotions (Panksepp & Bernatzky, 2002; Peretz et al., 1998). A patient with a large lesion of the temporal and frontal cortices had severe impairments in music perception but intact capacity for music appreciation (Peretz et al., 1998). A number of evolutionarily old brain regions, such as the amygdala, insula, and striatum, have consistently been implicated in music emotion induction and enjoyment (Blood & Zatorre, 2001; Blood et al., 1999; Brattico et al.,

2013; Koelsch, 2014; Koelsch et al., 2006; Salimpoor et al., 2011). Indeed, in dementia patients, atrophy of the insula, amygdala, and temporoparietal regions was associated with impaired music emotion recognition (Hsieh et al., 2012; Omar et al., 2011). These studies imply that music could elicit emotions by activating subcortical regions, though many cortical mechanisms are involved in various other aspects of music information processing and appreciation (Brattico et al., 2013; Koelsch, 2014).

However, imaging studies of music emotions have focused on the explicit processing of emotions with subjects focusing on the emotional content of the music (Brattico et al., 2011; Koelsch et al., 2006; Koelsch et al., 2013; Mitterschiffthaler et al., 2007). The main structures associated with music emotion perception include the bilateral auditory cortices, orbitofrontal cortex, cingulate cortex, parahippocampal gyrus, right nucleus accumbens, and the bilateral amygdala (Koelsch, 2014). A few functional magnetic resonance imaging (fMRI) studies (Menon & Levitin, 2005; Pereira et al., 2011) found evidence of activity in emotion-related brain structures even if subjects were not concentrating on an emotion-related task during scanning. However, those studies did not include an explicit emotion-listening condition. Thus, despite its prevalence in music usage in everyday life, such as for mood regulatory purposes or for influencing consumer's behavior, implicit emotion processing in music as opposed to explicit music emotion processing has not yet been addressed from a neural perspective.

The implicit and explicit processing of emotional visual stimuli has been studied extensively with facial expressions, typically by comparing conditions in which subjects classified the gender of face pictures presented for around 700 msec to 3 sec, or classified the emotions expressed by the faces. Implicit face processing employs limbic and emotion-related cortical areas, such as the insula (Critchley et al., 2000; Fusar-Poli et al., 2009; Keightley et al., 2003), the anterior cingulate cortex (Keightley et al., 2003; Williams et al., 2006), the inferior

prefrontal cortex (Critchley et al., 2000), and subcortical areas, such as the amygdala (Keightley et al., 2003; Williams et al., 2006). On the other hand, explicit face processing activates cortical areas along the temporal, occipital, and frontal lobes. These regions include the inferior/middle temporal gyri (Critchley et al., 2000; Scheuerecker et al., 2007), related to processing facial expressions and movements (Puce et al., 1998), and limbic areas such as the dorsal anterior cingulate cortex (Scheuerecker et al., 2007; Williams et al., 2006), involved in the regulation of emotion responses (Etkin et al., 2011), and the medial prefrontal cortex (Fusar-Poli et al., 2009; Scheuerecker et al., 2007; Williams et al., 2006], related to self-reflective thought and appraisal (Smithz & Johnson, 2007). In addition, a number of visual association areas, such as the fusiform gyrus, the inferior and middle occipital gyri, and the lingual gyri (Fusar-Poli et al., 2009; Scheuerecker et al., 2007), show increased activation in explicit compared with implicit emotion processing. Subcortically, the explicit processing of facial expressions or other emotional pictures activates the hippocampus (Critchley et al., 2000; Fusar-Poli et al., 2009) and in one study also the bilateral amygdala (Fusar-Poli et al., 2009; Scheuerecker et al., 2007; but for the opposite finding, showing a larger involvement of the amygdala during implicit processing, see Critchley et al., 2000).

In the auditory modality, several studies have addressed explicit and implicit emotion processing conveyed through prosody ('melody of speech'). Findings are again conflicting, likely depending on the study design and stimuli. Nonetheless, the implicit processing of brief prosody stimuli (typically lasting less than 1 sec) seems to engage temporal areas, such as the superior temporal gyrus and sulcus (Frühholz et al., 2012; Bach et al., 2008; Grandjean et al., 2005; Sander et al., 2005), which are sensitive to voices and prosodic features. Implicit processing also recruits the right inferior parietal lobule (Bach et al., 2008; Ethofer et al., 2009; Sander et al., 2005; Wildgruber et al., 2005), a heterogeneous area involved in the storage of phonetic and intonational acoustic information (Wildgruber et al., 2002), and

frontal areas such as the inferior frontal gyrus (Frühholz et al., 2012), involved in evaluative judgments of affective prosody (Schirmer & Kotz, 2006). Subcortical areas have also been implicated including the parahippocampal gyrus (Frühholz et al., 2012; Sander et al., 2005) and the amygdala (Bach et al., 2008; Ethofer et al., 2009). Explicit prosody processing also recruits temporal areas (Bach et al., 2008; Ethofer et al., 2009; Frühholz et al., 2012; Wildgruber et al., 2005) and frontal areas, such as the inferior frontal gyri (Bach et al., 2008; Ethofer et al., 2009; Frühholz et al., 2012) and the orbitofrontal cortex (Ethofer et al., 2009; Sander et al., 2005; Wildgruber et al., 2005). Subcortically, activation has also been observed in the parahippocampal gyrus and the amygdala in at least one study (Frühholz et al., 2012). In this experiment, we used fMRI to investigate the neural processing of emotions in music while participants performed a primary task focused on the emotional content (explicit condition) or diverted away from it (implicit condition). We hypothesized that cortical and subcortical areas of the limbic system would be important in implicit emotion processing as they are evolutionarily old areas associated with basic emotion responses even in non-primate mammals (Damasio & Carvalho, 2013). We thus expected to observe limbic activity during implicit processing, substantiating the hypothesis that musical emotions can be similar to reflexes, subcortically generated and not requiring the subject's awareness (Peretz, 2006; Juslin, 2013; Panksepp & Bernatzky, 2002). In contrast, for explicit emotion processing, we predicted recruitment of prefrontal areas, such as the dorsolateral and ventrolateral prefrontal cortex, related to the conceptual act of categorizing emotions (Koelsch, 2014; Smith & Jonides, 1999; Burunat et al., in press), and parietooccipital areas, important for attentional focusing (Ptak, 2012).

2. Materials and methods

2.1 Participants

Sixty-three subjects were recruited to this study through various email lists of the University of Helsinki, Helsinki, Finland and Aalto University, Espoo, Finland. Inclusion criteria were an absence of hearing problems, neurological problems, and psychopharmacological medication. Before participating, subjects were given information about the study, signed consent forms, and filled out an fMRI safety questionnaire. To compensate them for their time, participants were given a voucher for cultural and exercise activities for every half an hour of participation. In total, seven subjects were excluded from the analysis: three due to excessive movements during scanning, one due to technical issues and three because of neuroradiological abnormalities as diagnosed by a radiologist. Table S1 with the mean movement parameters per subject showing the cutoff can be found in the supplementary material.

The final sample consisted of 56 participants (mean age: 28.2 yrs \pm 8.21 SD yrs, range 20–53, 22 males, three left-handed). Eleven subjects had played a musical instrument for 5 years or more, and of those eight still played music (at least two hours per week). This study was approved by the “Koordinoiva” ethical committee of Helsinki and Uusimaa Hospital District and carried out in accordance with the Declaration of Helsinki.

- Insert Figure 1 around here -

2.2 Stimuli

The stimuli were musical excerpts taken from a movie soundtrack database; the music clips in this database were previously rated on a wide range of affective categories and validated for their target emotion (Eerola et al., 2011). Film music stimuli were chosen for this study because music in movies is composed to represent and induce emotions in listeners. We chose musical clips that were ranked highly for the target emotions (happiness, sadness, and fear) in the Eerola et al. (2011) study. Eighty-one musical stimuli were edited using Adobe Audition to last four seconds with a 500 ms fade-in and fade-out and normalized to each

other to match loudness levels as measured by the average root mean square (RMS) over the whole duration of the stimulus. We reduced the duration of the musical excerpts to keep the task as consistent as possible with previous studies of implicit processing (e.g., Bach et al., 2008; Critchley et al., 2000; Frühholz et al., 2012). However, we still kept the stimulus duration in the range of seconds rather than milliseconds (as in visual studies or behavioral studies on music emotion perception; see Filipic et al., 2010) to comply with previous music neuroimaging studies (e.g., Koelsch et al., 2006; Salimpoor et al., 2011; Brattico et al., 2011; however, see Pallesen et al., 2005, 2009 for studies on musical emotions using single chords lasting less than 1 sec), and to implicitly induce the desired emotions in the listeners and ensure robust brain activation.

To select the final stimuli, a separate group of 10 subjects who did not participate in the fMRI experiment rated the musical stimuli on nine different emotion categories (happiness, sadness, fear, anger, tenderness, pleasure, disgust, surprise, unclear, or other emotion; if they indicated “other emotion”, they were instructed to indicate the emotion). The ten best excerpts representing each of the three emotions—happiness, sadness and fear—were chosen. We analyzed subjects’ evaluations of the emotion category (happy, sad, fearful) during the acquisition of echo planar imaging (EPI) data for the explicit block for accuracy to confirm that they perceived the intended target emotion in each music clip. Two subjects’ responses were not recorded due to technical errors, and therefore the analysis of the behavioral responses is based on 54 subjects.

2.3 Paradigm

Prior to the actual experiment, the subjects completed a short training session with different stimuli in the scanner to familiarize themselves with the paradigm (Figure 1). The experiment is comprised of two tasks, implicit and explicit, each presented in a unique block as in previous studies using voices (e.g., Bach et al., 2008; Frühholz et al., 2012) or faces (e.g.,

Critchley et al., 2000; Scheuerecker et al., 2007). In the implicit processing task, we sought to mirror the non-affective (typically gender) task in studies of visual and vocal emotions. Thus, we aimed for an easy task that did not require any musical training and that forced the subjects' focus on a feature of the music not related to the emotional content or valence of the music in any way. Subjects were asked to mentally count the number of musical instruments in a clip (many, two or one), a task that requires musical knowledge that is accessible to the general population and does not relate to the affective content of the stimulus. Specifically, subjects were asked: "How many instruments do you hear in the music clip?". They had three answer choices: "one, two or many". In the explicit block, participants were asked "What emotion do you hear in the music clip?". The answers consisted of three emotion labels: "happiness, sadness or fear". The questions were explained orally to the subjects prior to the commencement of the session by one of the experimenters (BB). After three brief practice rounds, the question was presented visually once the experimental session began. Throughout each block, the three possible answers were presented as text on the screen. Each 4-sec stimulus was followed by a 5-sec answer period, during which subjects were instructed to answer the question by pressing one of three push buttons on an fMRI-compatible response box.

The thirty stimuli were randomized and presented once per block using Presentation software (Neurobehavioral Systems, Berkeley, CA). Button assignment was pseudo-randomized. After the first block, subjects were presented with the instructions for the second block and proceeded with the second half of the experiment after indicating that they understood the instructions. The order of the implicit and explicit blocks was randomized across participants.

2.4 Acoustic features

To study the effects of acoustic features, we used the MiRToolbox (Lartillot & Toiviainen, 2007) in a Matlab environment to broadly capture the timbral, tonal, and rhythmic aspects of

the stimuli. Each of the music clips was analyzed for 22 acoustic features that correspond to perceptual attributes and are well-studied in the psychoacoustic literature (Aucouturier & Bigand, 2013). The features were extracted from the stimuli on a frame-by-frame basis (for more details on computational feature extraction see Brattico et al., 2011; Eerola et al., 2011; Alluri et al., 2012). The values were converted to z-scores and grouped into six sets according to a classification implemented in Eerola et al. (2011) in order to minimize Type I errors resulting from multiple comparisons. The six sets included dynamic features (root mean square, RMS energy, and low energy), rhythm features (tempo and pulse clarity), timbre features (zero cross, centroid, brightness, spread, skewness, kurtosis, flatness, entropy, roughness, irregularity, and spectral flux), pitch features (chroma peak), tonality features (key clarity, mode, HCDF, and spectral entropy) and articulation features (attack time and attack slope).

Separate one-way ANOVAs with Emotion as the factor (three levels: happiness, sadness, fear) conducted on each acoustic feature revealed a significant main effect of Emotion for the dynamic feature set ($F_{2,27} = 8.909$; $p = .001$), timbre feature set [$F(2,27) = 6.156$, $p = .01$], and tonality feature set ($F_{2,27} = 17.741$, $p = .00001$). Based on these results, the relevant acoustic features were included as regressors of no interest in the whole-brain analysis.

2.5 FMRI acquisition

This study was conducted in the Advanced Magnetic Imaging (AMI) Centre at Aalto University, Espoo, Finland. The stimuli were delivered to subjects via high-quality MR-compatible insert earphones. The sound level of the stimuli was adjusted for each subject so that the stimuli were audible above the scanner noise, but the volume stayed within safety limits (below 80 dB). Additional hearing protection was used (noise-attenuating headphones), and the scanner noise was further attenuated with foam cushions.

Scanning was performed using a 3-T MAGNETOM Skyra whole-body scanner and a standard 20-channel head-neck coil (Siemens Healthcare, Erlangen, Germany). An interleaved gradient echo-planar imaging (EPI) sequence (TR = 2 s; echo time = 32 ms; flip angle = 75°) sensitive to blood oxygen level-dependent (BOLD) contrast was used to acquire 33 oblique slices allowing coverage of the whole brain (field of view = 192×192 mm; 64×64 matrix; slice thickness = 4 mm; voxel size = 3 mm x 3 mm x 4 mm; spacing = 0 mm). High-resolution anatomical T1-weighted MR images (176 slices, field of view = 256 mm; 256×256 matrix; voxel size = 1 mm x 1 mm x 1 mm; spacing = 0 mm) were collected after the fMRI tasks.

2.6 FMRI Analysis

The preprocessing and the statistical analysis of the whole-brain imaging data were performed using Statistical Parametric Mapping (SPM8) and Voxel-Based Morphometry (VBM; Wellcome Department of Imaging Neuroscience, London, UK) on a Matlab platform, following a routine used in previous studies (Alluri et al., 2012; Brattico et al., 2011; Brattico et al., 2016). Images for each participant were realigned to adjust for movement between volumes, resampled to a 2-mm isotropic voxel size, and then segmented with VBM into gray matter, cerebrospinal fluid, and white matter images, which were normalized spatially onto the Montreal Neurological Institute (MNI) a priori tissue template of the gray matter according to a 12-parameters affine transformation. The final preprocessing step included spatial smoothing with a Gaussian filter of 6 mm full-width at half maximum (FWHM). The normalization using segmented gray matter images as an intermediate step was chosen for its superiority over the direct normalization of EPI images to the MNI template according to pilot tests. Smoothed, normalized brain volumes were screened to determine whether they met the criteria for high quality and scan stability as determined by small motion correction (< 2 mm translation and < 2° rotation). The data were filtered temporally using a high-pass

filter of 128 Hz to minimize scanner drift. The fMRI responses were modeled using a canonical hemodynamic response function (HRF), and the six movement parameters were used as regressors of no interest.

Following preprocessing, individual contrasts for each emotion over baseline (happy>baseline, sad>baseline, fear>baseline) were computed for each type of processing (explicit and implicit) for each subject. The baseline consisted in 5-sec periods between stimuli. These individual contrast images (i.e., the weighted sum of the beta images) were entered into a second-level random effects model to account for scan-to-scan variability and participant-to-participant variability. To analyze the effects of implicit vs. explicit experimental condition on the processing of sad, happy and fearful musical emotions, we used a general linear model (GLM) with Emotion (three levels: sad, happy and fearful) and Processing Type (two levels: explicit, implicit) as within-subject factors. As there were an unequal number of male and female subjects, gender was also included as a regressor of no interest in all analyses. Additionally, since some acoustic features were found to differ between emotional categories of the musical stimuli, these features were included as regressors of no interest in the GLM for the fMRI responses. The inclusion only slightly affected the results for the main effect of Emotion, whereas it did not have any effect on the main effect of Processing type since the same stimuli were presented in the implicit and explicit processing conditions, leaving the acoustic features unvaried.

Family-wise error (FWE) correction and a minimum cluster size of 6 voxels were applied to protect against false positive results. The anatomical structures were labeled using the AAL Toolbox for SPM (Tzourio-Mazoyer et al., 2002), favoring the labeling with the highest percentage of cytoarchitectonic probabilities (>70%) for the cluster peaks and the highest overlap with the AAL structures for the cluster volumes. All areas are reported using MNI coordinates (from the Montreal Neurological Institute atlas of 152 averaged brains).

To determine the significant differences in activity and to study the direction of the main effects by means of post-hoc t-tests, we adopted two separate procedures. For the main effect of Processing Type, which included only two levels, we conducted t-tests contrasting implicit>explicit processing and explicit>implicit processing. For the main effect of Emotion, containing three separate levels (happiness, sadness, fear), we extracted the preprocessed signal change obtained with SPM of the significant clusters of activation that survived the FWE correction by using the MarsBaR Region of Interest (ROI) toolbox for SPM (marsbar.soundforge.net; Brett et al., 2002). For this BOLD signal change (parameter estimate) extraction, we used a sphere with a 10 mm radius centered on the local maximum coordinates of the clusters of interest (see Table 1 for the cluster coordinates of the main effect of Emotion; for a similar procedure within auditory neuroimaging, see, e.g., Neufeld et al., 2012; Schulze et al., 2010). Subsequently, we conducted paired t-tests between stimulus categories on the mean signal change and retained the results that survived Bonferroni correction.

3. Results

3.1 Behavioral results

Subjects' responses for emotion categories were evaluated for accuracy. Analysis of subjects' responses in the explicit task showed that mean correctness amounted to 28.22 ± 1.87 SD correct out of 30 (range 21–30; median: 29). Response accuracy was 94.1 ± 6.23 SD %.

The accuracy in the implicit task was not statistically investigated since it was not part of the study hypothesis and was rather meant as a distractor from the emotional content of the stimuli. Our inspection of the data confirmed that subjects responded to each trial, although not always according to our predictions, because fewer than 10 (out of 56) subjects reported in the informal post-session briefing that they were not clear whether they should respond to the number of instrument families present in the music clip or the number of actual

instruments.

3.2 Main effect of Emotion

As demonstrated in Figure 2 and Table 1, the stimuli activated large clusters in the bilateral superior temporal gyri, particularly the temporal poles. In addition, smaller clusters of activation were obtained in the left anterior cingulate cortex and the nearby supplementary motor area, the right-sided orbitofrontal cortex and the left hemispheric middle frontal gyrus (although this cluster includes only 11% voxels within the gray matter and the rest falls into the white matter). Within the limbic system, a significant cluster was found in the left parahippocampal gyrus neighboring the amygdala and hippocampus. Weaker hemodynamic activity was also observed in the right amygdala, hippocampus, parahippocampal gyrus, and caudate nucleus, but it remained under the FWE correction threshold.

For identifying the direction of the main effect of Emotion from the GLM, we conducted post-hoc paired t-tests on the mean of the BOLD signal change extracted from the six significant clusters obtained (see Table 2 for the statistical values of these t-tests and Figure 2 for the means and standard error of the mean). Results revealed that the BOLD signal change in the bilateral superior temporal gyri was significantly more positive for happy music than for sad and fearful music ($p < .0001$ for all), whereas responses to sad and fearful music did not differ from each other. Also for the left subcortical mediotemporal cluster including the parahippocampal gyrus, the extracted signal change was larger in response to happy music than to sad and fearful music ($p < .01$ for both), which did not differ from each other. The extracted signal change in the right orbitofrontal cortex was most negative for fearful than happy and sad music ($p < .007$ for both), and there was a non-significant tendency for a difference even between BOLD signal to fearful and sad music ($p = .01$). For the left anterior cingulate cluster, the BOLD signal change was significantly more positive for sad and fearful music than for happy music ($p < .001$ for both), whereas it did not differ between fearful and

sad music. In turn, the extracted signal change from the left middle frontal gyrus was more positive for fearful and sad music than for happy music ($p < .001$ for both), with no difference between the signal to sad and fearful music. At a much smaller scale, the signal change for the cluster in the supplementary motor area also differed significantly between emotion categories, with happy music eliciting significantly more positive responses than sad and fearful music ($p < .001$ for both), which in turn did not differ significantly between each other.

3.3 Main effect of Processing Type

The main effect of Processing Type activated large and highly significant clusters in the right lobule VI of cerebellum, pars opercularis of the left inferior frontal gyrus, right inferior parietal lobule, right angular and superior occipital gyri, and bilateral middle frontal gyrus.

All these clusters were particularly recruited by implicit processing as contrasted with explicit processing, as revealed by t-contrast implicit > explicit processing (see Figure 3 and Table 1). Smaller cortical clusters were also activated, particularly for implicit > explicit processing, in frontal and temporal areas, namely in the bilateral middle and superior frontal and precentral gyri, and the left inferior parietal lobule. Subcortically, the right caudate nucleus extending to the pallidum of the lenticular nucleus were recruited especially during implicit (>explicit) processing of musical emotions.

The extensive clusters in the bilateral inferior occipital gyri, extending to the fusiform and lingual gyri and to the cerebellar crus I, as well as the clusters of activation in the bilateral medial superior frontal gyri were associated with explicit processing instead, as revealed by the t-contrast explicit > implicit processing (Figure 3, Table 1).

4. Discussion

To our knowledge, this is the first study that addresses the neural correlates of implicit emotion processing in music as contrasted with explicit emotion classification. While a

growing body of research has explored the brain substrates of musical emotions, so far the implicit processing of emotions in music has remained neglected despite music often being used as an accompaniment to another activity. Behavioral data confirmed that even when shortened, the music soundtrack clips from the database by Eerola et al. (2011) were able to convey sad, fearful, and happy emotions. In implicit compared to explicit processing, we found large cortical areas of activity in the temporal, frontal, and parietal lobes as well as in reward-related areas. In contrast, explicit processing activated temporal, frontal, and occipital lobes. Overall, each emotion was also characterized by a distinct network of neural activity, including auditory and limbic areas, which could not be attributed to variations in acoustic features since the acoustic features were regressed out from the analysis.

4.1 Implicit vs. explicit processing

The largest clusters of activation during the implicit task were observed in the bilateral inferior parietal lobule extending into the occipital and angular gyri. Interestingly, activity in the inferior parietal lobule is consistent with explicit processing of emotional vocal and visual stimuli (Wildgruber et al., 2005; Scheuerecker et al., 2007) and with the implicit processing of prosody (Bach et al., 2008; Wildgruber et al., 2005). The right inferior parietal lobule has also been associated with musical emotion processing, particularly with respect to exciting pleasant versus relaxing pleasant music (Flores-Gutierrez et al., 2007) and with music performer expressivity (Chapin et al., 2010). A patient with an infarct in the right inferior parietal lobule reported musical anhedonia, or, in other words, the inability to have emotional experiences in response to music (Satoh et al., 2011). Thus, based on previous studies and on our current findings, the inferior parietal lobule seems to be important in the implicit affective experience of auditory stimuli.

Several activations associated with the processing type were also found in the bilateral dorsolateral prefrontal regions: the most significant were in the inferior and middle frontal

gyri, particularly during implicit processing of music. Studying the processing of prosody, Frühholz et al. (2012) observed strong bilateral inferofrontal activation in the implicit condition (gender identification), although this activity was centered more ventrally than the one observed here. Similarly, studies of facial implicit processing have also found left-sided inferofrontal activations (Critchley et al., 2000). In contrast, other studies have found right inferior frontal gyrus activation in the explicit condition (Bach et al., 2008; Ethofer et al., 2009). Overall, the inferior frontal gyrus and the other frontal clusters activated during implicit processing of musical emotions belong to the dorsolateral prefrontal cortex (DLPFC), which is generally involved in working memory (Smith & Jonides, 1999), response selection (Bunge et al., 2002), and rule-guided behavior (Mansouri et al., 2009), but also in conscious emotion regulation (Kohn et al., 2014), and has been observed in response to music emotions (Khalifa et al., 2005). Indeed, the neighboring activity in premotor areas of the frontal gyrus is commonly observed in response to music-induced emotions (Blood & Zatorre, 2001; Mitterschiffthaler et al., 2007; Mizuno & Sugishita, 2007).

In this study, processing type did not modulate amygdala activity consistently. A non-significant tendency for larger amygdalar activation in the left hemisphere during implicit emotion processing as opposed to explicit processing was obtained using a region-of-interest approach (see Supplementary Material). We speculate that the overall large recruitment of the amygdala during music listening in our experiment might have attenuated the differential effect of processing type. Other studies have revealed conflicting results. Subcortical areas have been hypothesized (Lane, 2008) to be important in implicit emotion processing as they are evolutionarily older areas associated with basic emotion responses, even in non-primate mammals (Damasio & Carvalho, 2013). Similarly, theories of brain basis of music appreciation suggest that subcortical areas, like the amygdala, are crucial to early emotional reactions to music (Brattico et al., 2013; Peretz, 2010).

During implicit musical emotion processing we also found a significant subcortical activation in the right caudate nucleus extending to the pallidum. The caudate nucleus is related to implicit learning or conditioning (Etkin et al., 2011) and reward-based learning (Haruno et al., 2004; Seger & Cincotta, 2005) and belongs to the reward circuit for motivational behavior (Delgado et al., 2004; Salimpoor et al., 2011). This neural activity complies with our hypothesis that during implicit processing of emotional music clips, the rewarding aspects of music are less inhibited by conscious categorization, making the subcortical activity more visible. These findings provide a neural basis for the behavioral effects of music on, e.g., consumers' decision making in a purchasing situation (Milliman, 1982; 1986), driving game performance (North & Hargreaves, 2008), or other behavior relying on learning from rewards (Gold et al., 2013).

Furthermore, the implicit processing of musical emotions recruited lobule VI of the right posterior cerebellum, previously linked to limbic functions (Schmahmann, 2004), providing some support of our hypothesis of the larger involvement of evolutionarily ancient brain areas during the unintentional processing of emotions in music. Damage to the posterior cerebellum and the vermis has been related to affective symptoms, such as the blunting of emotions and disinhibited behavior, and the size of the vermis correlates with ADHD and psychotic disorders (Schmahmann, 2004). Thus, the posterior cerebellum seems to play a role in the implicit processing of musical emotions.

4.2 Explicit vs. implicit

Explicit emotional classification activated several clusters belonging to the bilateral dorsomedial prefrontal cortex (DMPFC). This area has consistently been associated with emotion processing (Kober et al., 2008; Lindquist et al., 2012; Phan et al., 2002; Vytal & Hamann, 2010), also in the music domain (Khalfa et al., 2005). The cluster overlapped bilaterally with a cluster found by Williams et al. (2006) during the explicit processing of

fearful faces. It has been suggested that some parts of the DMPFC are active during the perception of emotion, whereas others are active during emotional experience (Lindquist et al., 2012). Hence, this area seems to be particularly important in the attentive perception and classification of emotions during music listening. Additionally, large bilateral clusters in the visual areas were activated during explicit processing of emotions and deactivated during implicit processing, most likely as a consequence of the conscious process of attributing an affective concept and verbal label to the music clips heard. A previous study with frontotemporal dementia patients showed the association between impaired recognition of musical (and facial) emotions with gray matter loss of parietooccipital areas (Omar et al., 2011), substantiating the relation between the neural correlates of visual and auditory sensory experiences.

4.3 Neural correlates of musical emotions

In this study, the neural structures that were overall recruited during listening to emotional music clips have been previously associated with musical emotions in a meta-analysis of 21 neuroimaging studies by Koelsch (2014): the bilateral auditory cortices, anterior cingulate cortex, orbitofrontal cortex, medial frontal gyrus, and, subcortically, the amygdala, hippocampus, and parahippocampal gyrus. Furthermore, here we observed differential brain activity to the three musical emotions expressed by the stimuli. Particularly, happy music (vs. sad or fearful music) produced significant and large activation in the primary and secondary auditory cortices, consistent with previous findings (Brattico et al., 2011; Koelsch et al., 2013; Park et al., 2014). This is unlikely to be due solely to the acoustic features of the music (Koelsch et al., 2013), and, together with the high accuracy in the behavioral classification of the emotional categories, supports our prediction that the music clips would clearly express emotions.

Happy music also generated a positive signal change in the left parahippocampal gyrus in the vicinity of the basolateral and superficial amygdala, which was significantly different from that in response to sad and fearful music. This limbic activity is consistent with neuropsychological studies with epileptic patients showing an impairment of happiness recognition in music only with left mesio-temporal resections encompassing the amygdala and, vice versa, an overestimation of musical pleasantness in patients with right amygdalar damage (Khalifa et al., 2008). A recent neuroimaging study further provides evidence of lateralized amygdala activity to music affect, with increased responses in the right amygdala only during listening to disliked music as opposed to liked music (Brattico et al., 2015). Overall, the sparse studies from the literature and our current results are in line with the hypothesis of music-specific lateralization of amygdala activity put forward by Brattico (2015), proposing that the left amygdala responds more to positively valenced auditory emotions and the right amygdala more responsive to negative ones. On the other hand, Koelsch and colleagues (2013) showed that bilateral amygdala takes approximately 8-10 seconds to activate fully and another 10 seconds to normalize in response to musical stimulation. Hence, the theorized amygdalar lateralization might be relevant only for brief musical stimulation used here and in previous studies (7 seconds music clips for the study by Khalifa et al., 2008 or 18 seconds music clips for the study by Brattico et al., 2015). Future experiments should test this hypothesis with realistic stimuli in a naturalistic listening condition (e.g., a tendency for functional connectivity of the left amygdala with a reward-related structure, such as the caudate, during naturalistic listening to pleasurable music was found for non-musicians by Alluri et al., 2015).

In contrast, negative emotions in music down-regulated the activity in the right-hemispheric orbitofrontal cortex, a brain structure known to control the experience of positive subjective feelings and pleasure (Berridge & Kringelbach, 2015), including in music (Blood et al., 1999;

Blood & Zatorre, 2001; Salimpoor et al., 2013). Furthermore, music clips expressing negative emotions, namely sadness and fear, recruited the left medial frontal gyrus and the left anterior cingulate cortex more than happy music. Activity in the medial frontal gyrus has been observed previously in association with sad music, mainly played in minor mode (Brattico et al., 2011; Khalfa et al., 2005; Vytal & Hamann, 2010). The anterior cingulate finding replicates what has been obtained in previous studies on negative music emotions, particularly sadness, both in music (Green et al., 2008) and also in other domains, as showed in a meta-analysis of 83 studies on discrete emotions (Vytal & Hamann, 2010).

We consider it a limitation of the study that we did not obtain any measures of autonomic nervous system changes and physiological arousal to provide additional evidence of the implicit processing of emotions during the instrument recognition task. This further development of the paradigm is of even greater importance considering that a minority of subjects in our experiment claimed to have some trouble understanding the task. However, our brain data, complemented with the highly successful emotion classification rates during the explicit task, validate the current paradigm. Future studies should, nevertheless, be conducted with a convergence of brain and physiological measures and include an even broader variety of musical emotions to replicate our findings. Similarly, the lack of the stimulus category of neutral music to compare with the emotional clips, or the restriction of the experiment to just three discrete emotions could be considered other pitfalls of the study. Shortening the music stimuli could help to address these limitations, but not before assuring the adequacy of brief stimuli to clearly express emotions even in an implicit processing condition. A further shortcoming of the current design consisted in using as baseline a relatively short inter-stimulus interval that was not only shorter than the decay time of the hemodynamic response to the preceding stimulation but even contained a motor response (button press). This choice was a trade-off between the need for collecting enough repetitions

of the brain responses to each emotional category and to the two experimental conditions on one side, and the amount of scanner time tolerable by participants on the other side.

Moreover, jittering of the inter-stimulus interval might be considered as a way to further increase the statistical power of this paradigm in future studies, although in a mixed event-related design with continuous acquisition as the current one, it is deemed as less mandatory.

4.4 Conclusions

The implicit processing of musical emotions extensively activated frontoparietal areas, including the right inferior parietal lobule and DLPFC as well as subcortical regions of the reward circuit, namely the bilateral caudate nucleus extending to the pallidum. There was no significant effect of processing type on the amygdala, not even when a ROI analysis was used, but a strong recruitment of the left parahippocampal gyrus (including voxels in the vicinity of the amygdala) for both experimental conditions and particularly in response to happy music clips. Indeed, we found a network of limbic and paralimbic regions differentially involved in the processing of sad, happy, and fearful emotions in music, emphasizing the role of the bilateral auditory cortices, the left parahippocampal gyrus and the supplementary motor area during positive music emotions (Brattico, 2015) and of the anterior cingulate cortex and middle frontal gyrus during the perception of negative emotions in music (e.g., Brattico et al., 2011; Khalifa et al., 2005; for a meta-analysis, see Koelsch, 2014). Although we did not obtain any measures of the autonomic nervous system changes to assess the emotional arousal during the implicit processing task, we observed highly successful emotion classification rates during the explicit task and obtained brain findings consistent with our hypotheses. In sum, our findings point to a role of frontoparietal, dorsolateral prefrontal, and striatal areas during the implicit processing of emotional experiences, requiring the dorsomedial frontal and visual areas for the explicit classification of musical emotions.

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Fig. 1. Experimental design. The experiment was conducted in two blocks. In the explicit block, subjects were asked to identify the emotional content of the stimulus. In the implicit block, subjects were asked to identify the number of instruments. After the presentation of each 4-sec music clip, subjects had 5 seconds to answer using the response box.

Figure 2. Main Effect of Emotion. (a) Brain activations to the main effect of emotions; (b) Graph depicts differential responses to emotions of happiness, sadness, and fear. All clusters depicted here are FWE corrected at $p < 0.05$. Bars represent the standard errors of the mean (SEM). Abbreviations: PHG: parahippocampal gyrus; ACC: anterior cingulate cortex; MFG: middle frontal gyrus; OFG: orbitofrontal gyrus; STG: superior temporal gyrus; SMA; supplementary motor areas; L_: left; R_: right.

Figure 3. Explicit vs. Implicit processing. (a) Brain activations elicited by contrasts: implicit>explicit and explicit>implicit; (b) Graph depicts differential activations to implicit or explicit processing. All clusters depicted here are FWE corrected at $p < 0.05$. Abbreviations: CB: cerebellum; CAU: caudate; ITG: inferior temporal gyrus; IPL: inferior parietal lobule; mSFG: medial superior frontal gyrus; MFG: middle frontal gyrus; IOG: inferior occipital gyrus; PreCG: precentral gyrus; SFG: superior frontal gyrus.

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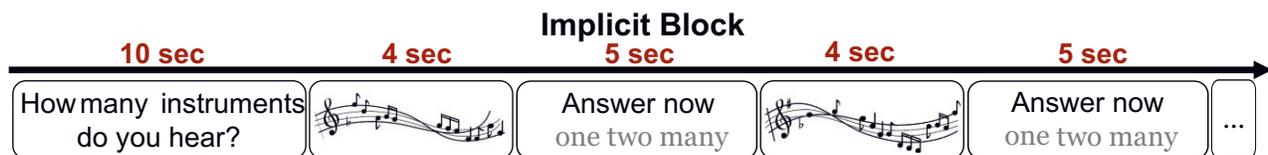
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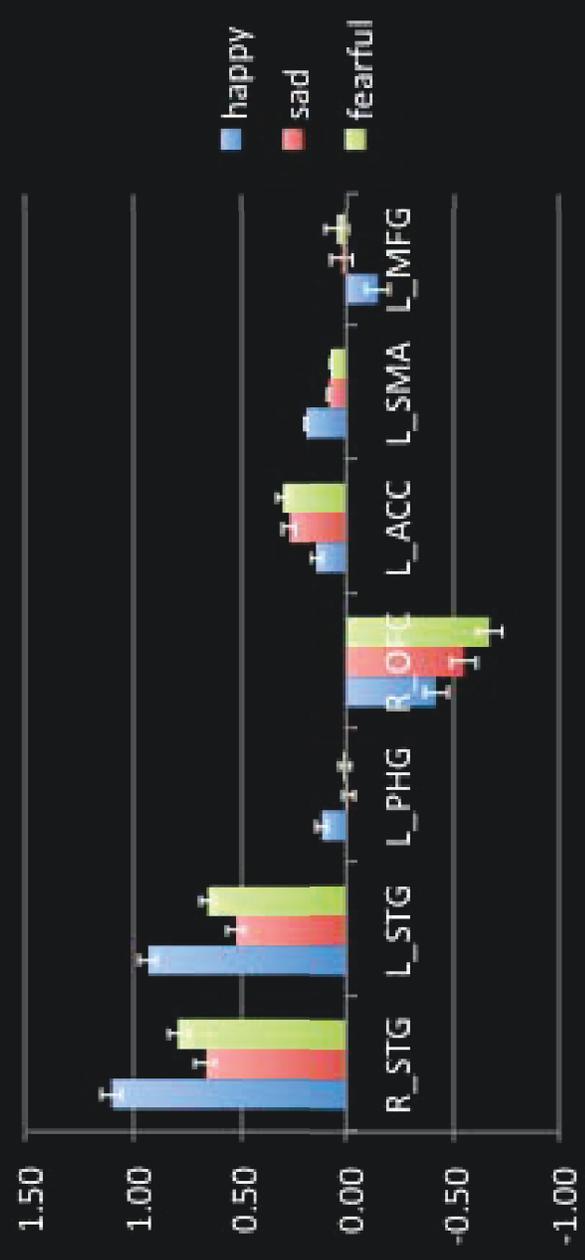
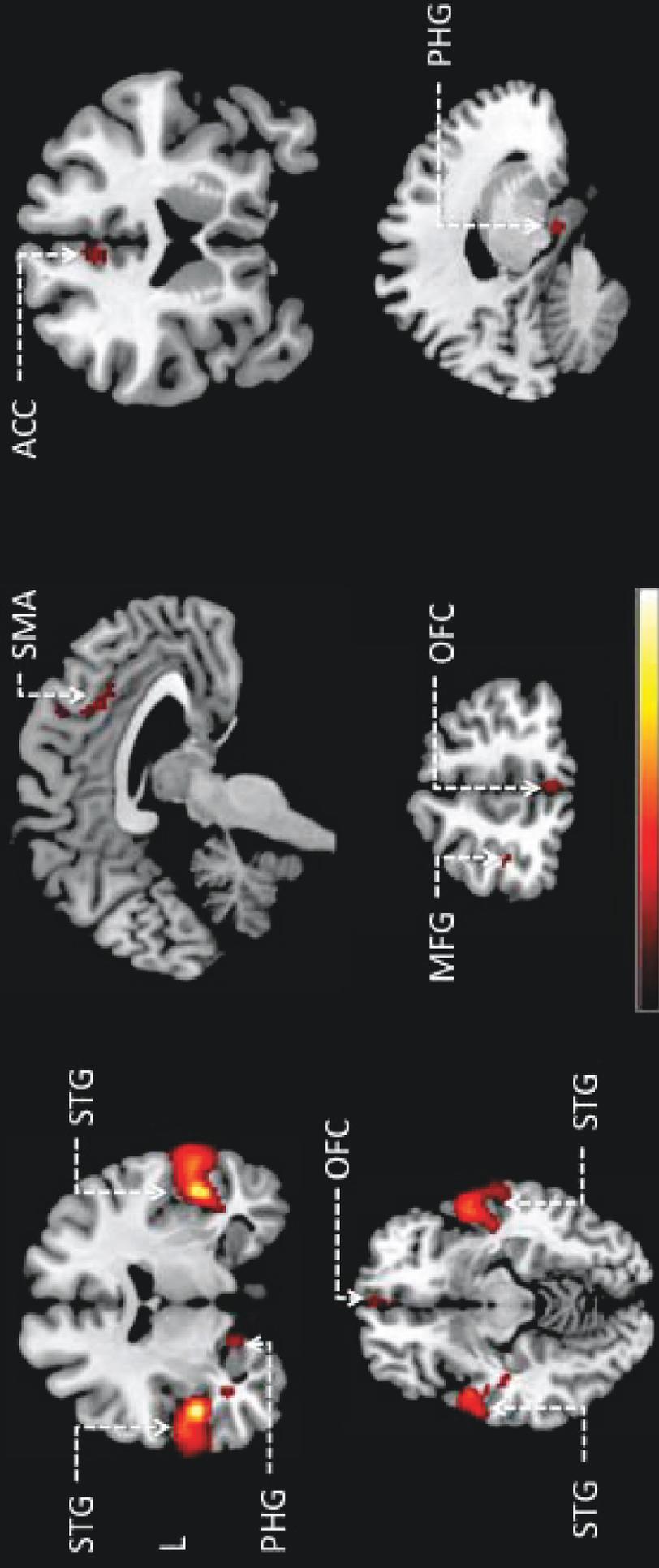
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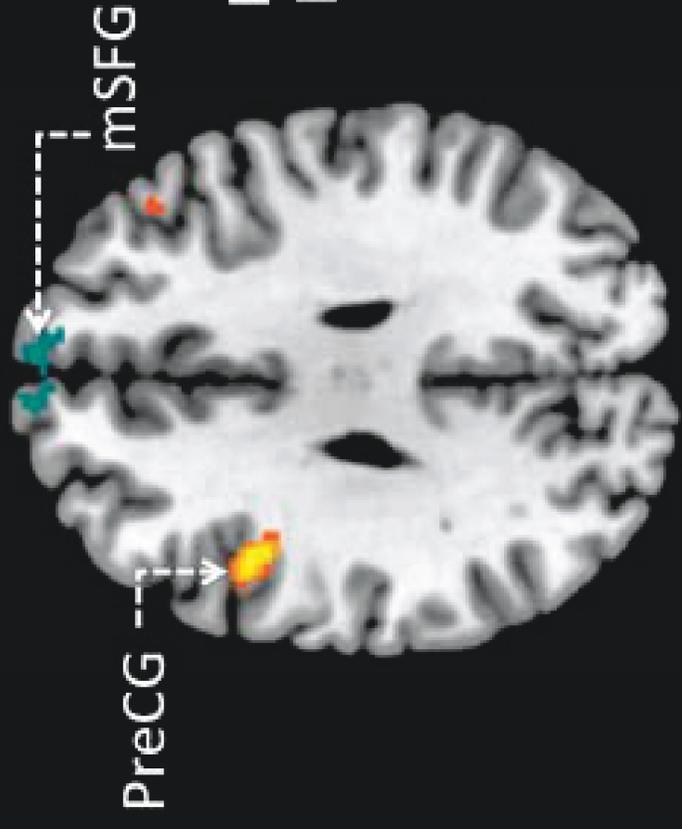
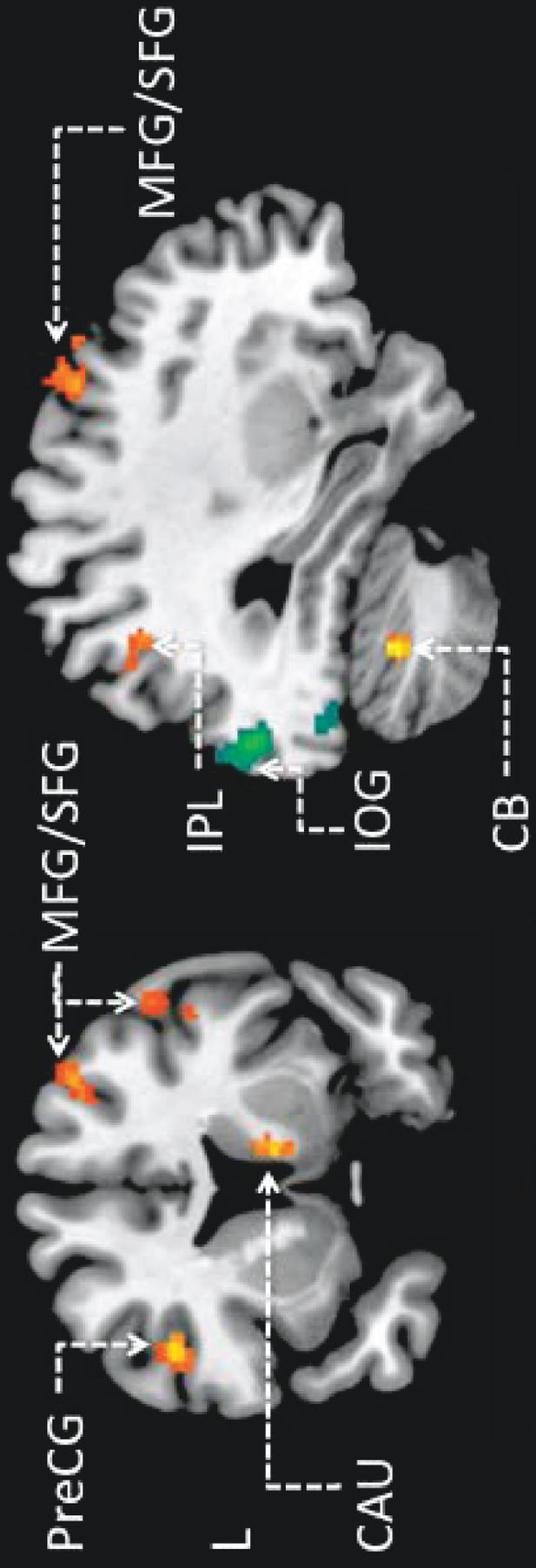


Table 1. Anatomical labels of the local maxima and volumes, coordinates and Z values, size (k) of the clusters from the main effects as obtained with GLM including acoustic features as regressors of no interest. Coordinates are in MNI space. Only clusters surviving the FWE corrected threshold of $p < .05$ and larger than 5 voxels. Abbreviations: STG = superior temporal gyrus, PHG = Parahippocampal gyrus, OFC = orbitofrontal cortex, ACC = anterior cingulate cortex, SMA = supplementary motor area, MFG = middle frontal gyrus, CB = cerebellum, IFGoper = inferior frontal gyrus (pars opercularis), IPL = inferior parietal lobe, Caudate Nucleus = CAU, Pallidum = PAL, SOG = superior occipital gyri, AG = angular gyrus, IOG = inferior occipital gyrus, FG = fusiform gyrus, LG = lingual gyrus, FG = fusiform gyrus, mSFG = medial superior frontal gyrus, R = right, L = left.

Region	L/R	x	y	z	k	Z
Main effect of Emotion						
STG	R	56	-2	-4	3174	>7.84
STG	L	-50	-10	-2	2262	>7.84
PHG	L	-18	-8	-19	26	6.50
OFC	R	2	48	-14	65	6.19
ACC	L	-6	24	36	42	5.95
SMA	L	-6	16	54	9	5.29
MFG	L	-32	48	8	9	5.19
Main effect of Processing Type						
a. Implicit>Explicit						
Lobule VI of CB	R	30	-64	-32	31	6.95
IFGoper	L	-44	8	30	84	6.92
IPL	R	48	-42	54	92	6.86
MFG	R	48	38	20	109	6.55
CAU, PAL	R	10	10	2	61	6.21
MFG	L	-26	4	63	16	5.96
AG, SOG	R	36	-76	42	79	5.90
ITG	L	-58	-54	-18	68	5.90
MFG, SFG	R	30	10	58	66	5.79
SFG	L	-2	20	44	11	5.45
IPL	L	-50	-34	38	6	5.37
PreCG	R	52	10	36	12	5.35
Main effect of Processing Type						
b. Explicit>Implicit						
IOG, FG, Crus I of CB	L	-40	-80	-12	939	>7.84
IOG, LG, FG	R	44	-78	-8	718	6.92
mSFG	L	-6	62	36	77	5.60
mSFG	R	12	62	36	58	5.60

Table 2. Results of the post-hoc paired t-tests for the main effect of emotion for each ROI. Abbreviations: t-stat = t statistic, SD = standard deviation of variable 1 minus variable 2, STG = superior temporal gyrus, PHG = Parahippocampal gyrus, OFC = orbitofrontal cortex, ACC = anterior cingulate cortex, SMA = supplementary motor area, MFG = middle frontal gyrus, R = right, L = left.

	t-stat	p-value	SD
happy vs. sad			
STG (R)	11.77	<0.0001	0.28
STG (L)	12.16	<0.0001	0.25
PHG (L)	6.96	<0.0001	0.13
OFC (R)	3.09	0.005	0.46
ACC (L)	-5.47	<0.0001	0.25
SMA (L)	5.91	<0.0001	0.02
MFG (L)	-4.54	<0.001	0.38
sad vs. fearful			
STG (R)	-6.54	<0.0001	0.15
STG (L)	-6.63	<0.0001	0.15
PHG (L)	-0.82	0.41	0.20
OFC (R)	2.53	0.01	0.12
ACC (L)	-1.09	0.28	0.27
SMA (L)	0.34	0.73	0.22
MFG (L)	-0.77	0.45	0.37
happy vs. fearful			
STG (R)	9.15	<0.0001	0.26
STG (L)	9.33	<0.0001	0.22
PHG (L)	6.21	<0.0001	0.19
OFC (R)	6.53	<0.0001	0.25
ACC (L)	-6.17	<0.0001	0.27
SMA (L)	6.12	<0.0001	0.21
MFG (L)	-4.75	<0.0001	0.42

Highlights

- Happy music activated the bilateral auditory cortices, left parahippocampal gyrus and supplementary motor area
- Sad and fearful music recruited the left anterior cingulate and middle frontal gyrus
- Implicit processing of music emotions activated dorsolateral prefrontal cortex, inferior parietal lobule, and caudate
- Explicit processing of music emotions activated occipital and dorsomedial prefrontal cortices

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