It is not always tickling: Distinct cerebral responses during perception of different laughter types

Diana P. Szameitat a,⁎,1, Benjamin Kreifelts a, Kai Alter b, André J. Szameitat c, Annette Sterr d, Wolfgang Grodd e, Dirk Wildgruber a

a Department of Psychiatry and Psychotherapy, University of Tübingen, Osianderstr. 24, 72076 Tübingen, Germany
b Department of Psychology, University of Surrey, Guildford GU2 7XH, UK
c Department of Psychology, Ludwig Maximilians University, 80802 Munich, Germany
d Department of Psychology, University of Surrey, Guildford GU2 7XH, UK
e Department of Neuroradiology, University of Tübingen, Hoppe-Seyler-Str. 3, 72076 Tübingen, Germany

A R T I C L E   I N F O

Article history:
Received 13 March 2010
Revised 1 June 2010
Accepted 9 June 2010
Available online 18 June 2010

Keywords:
Nonverbal
Social interaction
Emotion
Tickling
Joy
Taunt
fMRI

A B S T R A C T

Laughter is highly relevant for social interaction in human beings and non-human primates. In humans as well as in non-human primates laughter can be induced by tickling. Human laughter, however, has further diversified and encompasses emotional laughter types with various communicative functions, e.g. joyful and taunting laughter. Here, it was evaluated if this evolutionary diversification of ecological functions is associated with distinct cerebral responses underlying laughter perception. Functional MRI revealed a double-dissociation of cerebral responses during perception of tickling laughter and emotional laughter (joy and taunt) with higher activations in the anterior rostral medial frontal cortex (arMFC) when emotional laughter was perceived, and stronger responses in the right superior temporal gyrus (STG) during appreciation of tickling laughter. Enhanced activation of the arMFC for emotional laughter presumably reflects increasing demands on social cognition processes arising from the greater social salience of these laughter types. Activation increase in the STG for tickling laughter may be linked to the higher acoustic complexity of this laughter type. The observed dissociation of cerebral responses for emotional laughter and tickling laughter was independent of task-directed focusing of attention. These findings support the postulated diversification of human laughter in the course of evolution from an unequivocal play signal to laughter with distinct emotional contents subserving complex social functions.

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Introduction

Laughter is one of the few vocalizations shared by human beings and animals and, thus, might serve as a key to understanding the evolutionary development of human non-verbal vocalizations (Ross et al., 2009). Animal laughter is a reflex-like reaction restricted to the behavioral contexts of play and tickling (Darwin, 1872; Panksepp and Burgdorf, 2003; van Hooff, 1972). Human laughter is a more complex behavior, expressed not only in the context of play, but also in various emotional states (Giles and Oxford, 1970; Poyatos, 1993). This suggests that throughout evolution human laughter has adopted more complex communicative functions to reflect the increased complexity of human social interaction. We postulate that this is reflected in the neural signatures associated with the processing of different laughter types. Using fMRI we explored this idea by comparing the neural activities elicited during perception of tickling and emotional laughter.

Hypotheses regarding the functional neuroanatomical correlates can be derived from recent evidence on tickling and emotional laughter suggesting that both are fundamentally different in the complexity of their social meaning. In detail, tickling laughter is induced by touch and its adaptive value is to reinforce play behavior which in turn promotes social bonding (Panksepp and Burgdorf, 2003). Thus, tickling laughter in animals is an acoustic signal associated with an unequivocal positive impact on social coherence. Accordingly, the demand on social cognition processes in the listener may be assumed to be relatively low. In contrast, human laughter in distinct emotional contexts can incorporate diverse—even opposite—social functions, such as friendly approach in joy or rejection in taunt (Eibl-Eibesfeldt, 1970; Szameitat et al., 2009a). Thus, since the listener has to make inferences about the sender’s emotional state and intentions, the demand on social cognition processes is higher. Since social cognition processes, such as person perception and mentalizing, have been associated with neural activity in the anterior rostral medial prefrontal cortex (arMFC) (for a review see Amodio and Frith, 2005).
three types of laughter (joy, taunt, tickling). The actors were instructed to use auto-induction techniques, that is, they were advised to “get into” the corresponding emotional state by means of imagination and emotional recall (mental induction) as well as voicing and body movements (e.g., screaming, stomping; induction of bodily sensations). As soon as they strongly felt the emotional state, speakers started on their own accord to laugh freely without thinking about the expression of the laughter (for details see Szameitat et al., 2009a). Sequences containing speech, interjections, or background noise were excluded. From this initial stimulus sample only stimuli that were identified well above chance level in an independent behavioral study (Szameitat et al., 2009a) were included in the final stimulus set for tickling laughs and emotional (joy, taunt) laughs. The overall classification accuracy for the stimulus set was 69% (joy 68%, taunt 74%, tickling 65%). The stimulus set was balanced with respect to the expressed emotion and the speaker’s sex. All stimuli were normalized with respect to mean acoustic energy. Stimulus duration ranged from 3.2 to 9.2 s and was balanced across laughter types (mean duration ± SD: JOY: 7.56 ± 1.59 s; TAUNT: 7.48 ± 1.73 s; TICKLING: 7.74 ± 1.25 s). The resulting stimulus set consisted of 60 laughter sequences with 20 stimuli per emotion.

Experimental design

We employed an event-related design consisting of four blocks with 30 trials each. Stimuli were presented binaurally via magnetic resonance compatible headphones with piezoelectric signal transmission (Jancke et al., 2002). In the scanner room visual cues (classification scale, fixation cross) were back-projected (NEC MT 1030+) onto a translucent screen (picture size ∼ 80 × 65 cm) that was placed approximately 2.5 m from the subject’s head. The subjects viewed the screen via a mirror system mounted on the head coil.

We employed two tasks: explicit processing of emotional prosody (EXP), and implicit processing of emotional prosody (IMP). During the EXP task participants had to classify the laughter sequences according to the emotion expressed, i.e., joy, tickle, or taunt. During the IMP condition participants had to judge the number of bouts in the laughter sequence, that is 3, 4, or “W” (“W” = neither 3 nor 4, but any different number of bouts). A bout was defined as part of the laughter sequence from the start of a laughter sequence to the beginning of the first inspiration or the part between two inspirations. The tasks alternated across sessions and were balanced across subjects. The whole experiment consisted of 120 trials interspersed with 12 null events which were introduced to reduce effects of stimulus expectation and to improve the estimate of the hemodynamic baseline. The order of stimulus presentation was pseudo-randomized across and within sessions, balanced for expressed emotion, number of bouts, and sex of the speaker.

Each trial started with the stimulus presentation followed by a response window of 4 s during which a horizontal scale with three categories (joy, taunt, tickle/3, 4, W) was presented. Subjects conveyed their decisions by pressing one of three buttons on a fiber optic system (LumiTouch, Photon Control, Burnaby, Canada) using their right index, middle or ring fingers. To avoid lateralization effects caused by motor responses or possible laterality effects in the perception of emotionally valenced information the arrangement of categories on the scales was fully permuted resulting in six different scales for each task. The different scales were balanced across the subjects. The response window was followed by a variable inter-trial interval (range: 0.8–10.8 s) resulting in stimulus onset asynchronies ranging from 14 to 34 s (including null events with a duration of 16 s). Stimulus onset was jittered relative to the scan onset in steps of 0.5 s.

Prior to scanning, each task was practiced with 12 laughter sequences that were not part of the stimulus set of the main experiment. Subjects were instructed to not count aloud during the bout counting task.

Methods

Subjects

Eighteen subjects (nine males, mean age 26 years, SD 3.4 years) participated in the experiment. All participants were native German speaking, and all were right-handers, as assessed using the Edinburgh Inventory (Oldfield, 1971) and none had a history of neurological or psychiatric illness, substance abuse, impaired hearing or was on any medication. All the subjects’ vision was normal or corrected to normal.

Before taking part in the study, all participants gave written informed consent according to the guidelines of the University of Tuebingen Ethical Review Board. The study was accomplished according to the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Stimulus material

Eight professional actors (three males and five females) produced three types of laughter (joy, taunt, tickling). The actors were...
Image acquisition

A 1.5 T whole body scanner (Siemens AVANTO; Siemens, Erlangen, Germany) was employed to acquire functional MR images covering the whole cerebrum (field of view [FOV] = 192 × 192 mm, 24 slices, 4 mm slice thickness and 1 mm gap) using an echo-planar imaging (EPI) sequence (TR = 2 s, echo time [TE] = 40 ms, matrix = 64 × 64, and flip angle = 90°). To exclude measurements preceding the T1 equilibrium the first five EPI images were discarded. A static field map (TR = 487 ms, TE = 5.28 and 10.04 ms) was obtained in every subject for offline correction of distortions of the EPI images. High-resolution T1-weighted images were acquired using a magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence (FOV = 256 × 256 mm, 176 slices, 1-mm slice thickness, no gap, flip angle 15°, TR = 1980 ms, TE = 3.93 ms and matrix size = 2562). A total of 1,200 functional images (total scanning time: 40 min) was recorded for each subject.

Image analysis

Image analysis was carried out using SPM2 software (Welcome Department of Imaging Neuroscience, London, UK; http://www.fil.ion.ucl.ac.uk/spm/). Preprocessing of the functional MR images included motion correction, unwarping by use of a static field map, slice time correction to the middle slice (12th slice) and co-registration with the anatomical data. The transformation matrix for normalization to the Montreal Neurological Institute (MNI) space (Collins et al., 1994) was calculated on the basis of the structural T1-weighted 3-D data set of each subject and subsequently applied to the functional images. The functional images were re-sliced at resolution of 3 × 3 × 3 mm. The functional MR images were smoothed via a Gaussian filter with 10-mm full width half maximum (FWHM). For each trial a separate regressor was defined using a boxcar function with the length of the respective laughter sequence convolved with the hemodynamic response function. Events were time-locked to the stimulus onset. A high-pass filter with a cut-off frequency of 1/128 Hz was used to minimize low-frequency components. Serial autocorrelations of fMRI data were accounted for by modeling the error term as an autoregressive process with a coefficient of 0.2 (Friston et al., 2002) and an additional white noise component (Purdon and Weisskoff, 1998).

According to the hypotheses formulated in the introduction we defined the following anatomical regions of interest for the analysis of the functional MR data using the automated anatomical labeling tool integrated in the SPM software (Tzourio-Mazoyer et al., 2002): 1.) Stronger responses to emotional than to tickling laughter: medial frontal cortex (MFC) including the anterior cingulum (2274 voxels). 2.) Stronger responses to tickling laughter than to emotional laughter types: bilateral superior temporal sulcus (STS, 5487 voxels), for the purpose of statistical analysis conceptualized as the combination of superior and middle temporal gyrus (STG/MTG). 3.) Stronger responses during explicit than during implicit processing of laughter type: the orbitofrontal cortex (OFC), the inferior frontal gyrus (IFG), the medial frontal cortex (MFC) including the anterior cingulum and the posterior superior temporal sulcus (pSTS; here conceptualized as the posterior halves of STG and MTG) (7761 voxels). As activation foci may differ between studies we allowed for such spatial variability of activations by defining extensive ROIs. Significance levels of the results were calculated using a small volume correction (Worsley et al., 1996) based on the predefined ROIs.

Brain regions exhibiting stimulus-driven BOLD effects (averaged across tasks) with stronger responses to socially salient [joy [JOY], taunt [TAU]] than to tickle [TIC] laughter were identified by computing the contrasts (JOY > TIC) and (TAU > TIC), respectively. Moreover a conjunction analysis (Nichols et al., 2005) (JOY > TIC) ∩ (TAU > TIC) was applied to locate brain regions that are sensitive to social salience in laughter irrespective of the emotional valence of the socially significant laughter type.

In a parallel fashion, the reverse contrasts (TIC > JOY), (TIC > TAU) and the reverse conjunction (JOY > TIC) ∩ (TIC > TAU) were computed to identify brain regions within the ROIs with stronger responses to tickle laughter than to socially salient laughter. The statistical parametric maps were evaluated according to a conjunction null-hypothesis (Nichols et al., 2005).

Moreover, the contrasts JOY > TAU and TAU > JOY were analyzed to evaluate emotion specific activation effects.

Brain regions with stronger activations during explicit processing of laughter type were identified by the contrast EXP > IMP.

Statistical evaluation of group data was based on a second-level random effects analysis. Activations are reported at a height threshold of p < 0.001, uncorrected, and an extent threshold of k ≥ 25 voxels, corresponding to p < 0.05, corrected for multiple comparisons across the respective ROI. For the purpose of completeness also activations outside the predefined ROIs are reported at this threshold in form of a whole brain analysis.

As a second step in the analysis the mean parameter estimates were extracted from all significantly activated regions within the ROIs and submitted to a 2 × 2 ANOVA for repeated measures with laughter type (emotional [EMO = mean [JOY, TAU]] vs. TIC) and task (EXP vs. IMP) as within-subject factors in order to test whether the activity in the areas showing a stimulus-driven (or task-driven) effect is modulated by the task (or laughter type). Resulting p values were corrected for heterogeneous correlations (Geisser and Greenhouse, 1958). Separate post-hoc paired T-tests were employed for the comparison of the parameter estimates for the different tasks and stimulus types.

To explore the possibility that the effects of social salience observed in the conjunction analysis differed significantly between the two emotional laughter types (JOY, TAU) and to test the validity of collapsing JOY and TAU into the single category EMO within the framework of the ANOVAs we extracted the mean parameter estimates of the emotional laughter types (JOY, TAU) from the regions with significant stimulus- or task-driven effects. The parameter estimates for JOY and TAU were then compared using a paired T-test.

To exclude effects of erroneous task performance as source of the observed task-dependent activation a reanalysis of the functional imaging data was performed where only trials with correct responses were included in the analysis.

Results

Behavioral data

During both tasks all three categories could be discriminated well above chance level of 33% (EXP [mean hit rates ± SEM]: JOY: 76.7 ± 3.5%; TAU: 80.6 ± 3.5%; TIC: 63.3 ± 4.2%; IMP [mean correct bout counting trials ± SEM]: JOY: 89.4 ± 0.9%; TAU: 96.7 ± 1.0%; TIC: 74.2 ± 1.5%; all T(17) > 7.2, all p < 0.001). Mean hit rates for the laughter type categorization task were lower than for the bout counting task (EXP: 73.5 ± 2.5%; IMP: 86.8 ± 0.7%; T(17) = 4.9, p = 0.001), while mean reaction times were comparable between the two tasks (EXP: 808 ± 73 ms; IMP: 812 ± 52 ms, T(17) = 0.1, n.s.).

Effects of laughter type on brain activation (stimulus-driven effects)

The voxel-wise whole brain analysis of the differential activation through different laughter types revealed stronger responses to emotional laughter types than to tickling laughter in an anterior rostral mediofrontal region but also several occipital, occipito-temporal and posterior medial areas of the cortex while tickling laughter led to stronger responses than emotional laughter types within the superior temporal cortex, the temporoparietal junction and the dorsolateral prefrontal cortex (see Table 1).

The conjunction analysis (JOY > TIC) ∩ (TAU > TIC) revealed that the perception of emotional laughs (i.e. both emotional laughter types,
Table 1
Differential hemodynamic activation following the perception of emotional laughter types and tickling laughter.

<table>
<thead>
<tr>
<th>Laughter types</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-score (peak voxel)</th>
<th>Cluster size (voxel)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Joy→Tickle</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L parahippocampal gyrus/lingual gyrus/fusiform gyrus/hippocampus</td>
<td>−21</td>
<td>−42</td>
<td>−6</td>
<td>4.84</td>
<td>79</td>
</tr>
<tr>
<td>R fusiform gyrus/calcine gyrus/lingual gyrus/parahippocampal gyrus/hippocampus</td>
<td>30</td>
<td>54</td>
<td>3</td>
<td>4.16</td>
<td>31</td>
</tr>
<tr>
<td>R middle frontal gyrus/superior frontal gyrus</td>
<td>9</td>
<td>51</td>
<td>6</td>
<td>4.08</td>
<td>84</td>
</tr>
<tr>
<td>R medial superior frontal gyrus/R medial orbital frontal gyrus/R anterior cingulum/L medial superior frontal gyrus</td>
<td>−15</td>
<td>−42</td>
<td>57</td>
<td>4.00</td>
<td>45</td>
</tr>
<tr>
<td>L precuneus/middle cingulum/paracentral lobule</td>
<td>48</td>
<td>69</td>
<td>30</td>
<td>3.75</td>
<td>116</td>
</tr>
<tr>
<td>R middle occipital gyrus/middle temporal gyrus/angular gyrus</td>
<td>−42</td>
<td>−81</td>
<td>27</td>
<td>3.9</td>
<td>64</td>
</tr>
<tr>
<td>R inferior occipital gyrus/middle occipital gyrus/middle temporal gyrus/fusiform gyrus/inferior temporal gyrus</td>
<td>33</td>
<td>−75</td>
<td>−6</td>
<td>3.85</td>
<td>92</td>
</tr>
<tr>
<td>R angular gyrus/middle occipital gyrus/superior occipital gyrus</td>
<td>48</td>
<td>−69</td>
<td>30</td>
<td>3.75</td>
<td>116</td>
</tr>
<tr>
<td>Taunt→Tickle</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R parahippocampal gyrus/fusiform gyrus/hippocampus/lingual gyrus</td>
<td>27</td>
<td>−42</td>
<td>−9</td>
<td>4.26</td>
<td>69</td>
</tr>
<tr>
<td>R+L medial superior frontal gyrus/L medial orbital frontal gyrus/R+L anterior cingulum</td>
<td>9</td>
<td>54</td>
<td>9</td>
<td>3.96</td>
<td>180*</td>
</tr>
<tr>
<td>L middle temporal gyrus</td>
<td>−57</td>
<td>−12</td>
<td>−9</td>
<td>3.62</td>
<td>25</td>
</tr>
<tr>
<td>L middle cingulum/paracentral lobule/precuneus</td>
<td>−9</td>
<td>−42</td>
<td>51</td>
<td>3.6</td>
<td>45</td>
</tr>
<tr>
<td>L lingual gyrus/parahippocampal gyrus/fusiform gyrus/hippocampus</td>
<td>−24</td>
<td>−45</td>
<td>−3</td>
<td>3.45</td>
<td>26</td>
</tr>
<tr>
<td>(Joy→Tickle) AND (Taunt→Tickle)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R medial superior frontal gyrus/R anterior cingulum/L medial superior frontal gyrus</td>
<td>9</td>
<td>54</td>
<td>6</td>
<td>3.8</td>
<td>42*</td>
</tr>
<tr>
<td>Tickles→Joy</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R thalamus</td>
<td>6</td>
<td>−18</td>
<td>6</td>
<td>4.25</td>
<td>44</td>
</tr>
<tr>
<td>R superior temporal gyrus/supramarginal gyrus</td>
<td>63</td>
<td>−21</td>
<td>6</td>
<td>4.21</td>
<td>79*</td>
</tr>
<tr>
<td>L superior temporal gyrus</td>
<td>−48</td>
<td>−33</td>
<td>15</td>
<td>3.95</td>
<td>26</td>
</tr>
<tr>
<td>L supramarginal gyrus/inferior parietal gyrus/superior temporal gyrus</td>
<td>−60</td>
<td>−39</td>
<td>36</td>
<td>3.79</td>
<td>36</td>
</tr>
<tr>
<td>L superior temporal gyrus</td>
<td>−57</td>
<td>−15</td>
<td>6</td>
<td>3.67</td>
<td>35*</td>
</tr>
<tr>
<td>Tickles→Taunt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R superior temporal gyrus/supramarginal gyrus</td>
<td>63</td>
<td>−30</td>
<td>15</td>
<td>4.49</td>
<td>73*</td>
</tr>
<tr>
<td>R middle frontal gyrus/y inferior frontal gyrus pars triangularis</td>
<td>−39</td>
<td>42</td>
<td>21</td>
<td>4.36</td>
<td>74</td>
</tr>
<tr>
<td>R middle frontal gyrus/y inferior frontal gyrus pars opercularis/pars triangularis/precentral gyrus</td>
<td>42</td>
<td>3</td>
<td>39</td>
<td>4.16</td>
<td>111</td>
</tr>
<tr>
<td>R middle frontal gyrus/y inferior frontal gyrus pars opercularis/pars triangularis/precentral gyrus</td>
<td>−42</td>
<td>12</td>
<td>33</td>
<td>3.8</td>
<td>30</td>
</tr>
<tr>
<td>(Tickle→Joy) AND (Tickle→Taunt)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R superior temporal gyrus/supramarginal gyrus</td>
<td>66</td>
<td>−27</td>
<td>15</td>
<td>3.73</td>
<td>35*</td>
</tr>
</tbody>
</table>

Activations thresholded at $p<0.001$, uncorrected with a cluster size $k \geq 25$ voxels. Coordinates refer to the MNI system. *$p<0.05$, corrected for multiple comparisons across the respective ROIs (see Methods).

Fig. 1. A–C) Increased responses in the right aMFC during perception of emotional laughter than of tickle laughter: A) conjunction (JOY→TIC) ∩ (TAU→TIC); B) (JOY→TIC) = green, (TAU→TIC) = blue, conjunction = red ($p<0.001$, uncorrected, cluster size $k \geq 25$, corresponding to $p<0.05$, corrected multiple comparisons across the a priori anatomical ROI); C) Inspection of contrast estimates indicates the lack of a significant task effect or interaction between task and laughter type. Asterisks mark significant results ($**p<0.001$).

D–F) Stronger activation in the right middle STG during perception of tickle laughter than of emotional laughter: D) conjunction (TIC→JOY) ∩ (TIC→TAU); E) (TIC→TAU) = blue, conjunction = red ($p<0.001$, uncorrected, cluster size $k \geq 25$, corresponding to $p<0.05$, corrected). F) Inspection of contrast estimates reveals the lack of a significant task effect or interaction between task and laughter type. Error bars show standard error of the mean.
separately compared to tickling laughter) lead to increased responses within the arMFC (Fig. 1A, B; Table 1), while perception of tickling laughs, as investigated by the reverse contrast (TIC \( \cap \) JOY), lead to increased responses in the right STG (Fig. 1D, E; Table 1).

A 2×2 ANOVA (laughter type [EMO/TIC]×task [EXP/IMP]) on the mean parameter estimates of the respective activated clusters in the conjunction analyses in the arMFC (\( F(1,17)=31.7, p<0.001 \)) and STG (\( F(1,17)=35.3, p<0.001 \)) revealed that the main effect of laughter type was significant. Post-hoc tests showed that this effect was significant for both tasks within the arMFC with stronger responses to emotional laughter (EXP: \( t(17)=4.1, p<0.001 \); IMP: \( t(17)=4.1, p<0.001 \)) and within the STG with stronger responses to tickling laughter (EXP: \( t(17)=−3.2, p=0.004 \); IMP: \( t(17)=−6.2, p<0.001 \), two-tailed). Neither of the two regions exhibited a significant task effect or interaction of laughter type and task (Fig. 1C, F).

Paired t-tests based the mean parameter estimates of the respective activated cluster in the arMFC and STG showed that in none of the two regions there were significant differences between the two emotional laughter types joy and taunt (arMFC: \( t(17)=−0.7, p=0.51 \); STG: \( t(17)=0.4, p=0.73 \), two tailed).

Moreover, the whole brain analysis comparing responses to joyful and taunting laughter did not evidence any differential activation.

Impact of attention on brain activation (task-dependent effects)

Explicit emotional evaluation of laughter sounds (EXP \( \cap \) IMP) led to significantly stronger activations in the right posterior superior temporal sulcus (pSTS), the bilateral inferior frontolateral and orbitofrontal cortex (IFC, OFC), and the bilateral posterior rostral medial frontal cortex (prMFC) shown in Table 2 and Fig. 2E–H. Furthermore, stronger activation during explicit evaluation of laughter could be observed outside the a priori anatomical ROI within occipital and occipito-temporal brain regions and the cerebellum (Table 2).

However, in none of the regions reactive to the explicit emotional processing of laughter a significant effect of laughter type or an interaction between task and laughter type could be observed employing a 2×2 ANOVA (laughter type [EMO/TIC]×task [EXP/IMP]) on the mean parameter estimates of the respective activated region (Fig. 2A–D).

---

### Table 2

<table>
<thead>
<tr>
<th>EXP ( \cap ) IMP</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-score (peak voxel)</th>
<th>Cluster size (voxel)</th>
</tr>
</thead>
<tbody>
<tr>
<td>R inferior frontal gyrus pars triangularis/pars opercularis/pars orbitalis/insula/superior temporal pole/rolandic operculum</td>
<td>51</td>
<td>27</td>
<td>9</td>
<td>5.25</td>
<td>426*</td>
</tr>
<tr>
<td>L inferior frontal gyrus pars orbitalis/pars triangularis/insula</td>
<td>−42</td>
<td>24</td>
<td>−6</td>
<td>5.03</td>
<td>260*</td>
</tr>
<tr>
<td>R superior temporal gyrus/R middle temporal gyrus</td>
<td>45</td>
<td>−45</td>
<td>3</td>
<td>4.54</td>
<td>105*</td>
</tr>
<tr>
<td>R middle occipital gyrus/superior occipital gyrus/calcarine/cuneus</td>
<td>27</td>
<td>−87</td>
<td>18</td>
<td>4.44</td>
<td>216</td>
</tr>
<tr>
<td>R + L medial superior frontal gyrus/R + L supplementary motor area</td>
<td>3</td>
<td>39</td>
<td>48</td>
<td>4.42</td>
<td>154*</td>
</tr>
<tr>
<td>R fusiform gyrus/lingual gyrus</td>
<td>30</td>
<td>−60</td>
<td>−3</td>
<td>3.74</td>
<td>63</td>
</tr>
<tr>
<td>L middle frontal gyrus/inferior frontal gyrus pars triangularis/pars opercularis</td>
<td>−42</td>
<td>21</td>
<td>33</td>
<td>3.54</td>
<td>34</td>
</tr>
<tr>
<td>R + L cerebellum/cerebellar vermis/R + L lingual gyrus</td>
<td>12</td>
<td>−81</td>
<td>−18</td>
<td>3.44</td>
<td>34</td>
</tr>
</tbody>
</table>

Activations thresholded at \( p<0.001 \), uncorrected with a cluster size \( k \geq 25 \) voxels. Coordinates refer to the MNI system. \( *p<0.05 \), corrected for multiple comparisons across the a priori anatomical ROI (see Methods).

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Fig. 2. (E–H) Stronger activation during explicit than during implicit processing of laughter prosody (\( p<0.001 \), uncorrected, cluster size \( k \geq 25 \), corresponding to \( p<0.05 \), corrected for multiple comparisons across the a priori anatomical ROI). (A–D) Inspection of mean contrast estimates reveals the lack of a significant effect of laughter type or interaction between task and laughter type in all investigated regions. Error bars show standard error of the mean.
The reanalysis of the data including only correct trials performed to exclude effects of erroneous task performance as driving source of the observed effects showed that stronger responses during explicit processing of laughter prosody remained significant in all activated clusters identified in the initial ROI-analysis (Table 3). Moreover, the absence of significant stimulus-effects or interactions between laughter type and task within these regions was confirmed when incorrect trials were excluded from the analysis.

### Discussion

The present data confirmed our hypothesis of distinct neural activation patterns during perception of tickling and emotional laughter associated with different demands on social cognition and acoustic processing. The findings support the notion that emotional laughter may have evolved and diversified in humans to accommodate increasingly complex social interactions.

We found that emotional laughter showed increased activation in the aMFC in contrast to tickling laughter. Based on a meta-analysis of fMRI studies (Amodio and Frith, 2006) it has been assumed that within the MFC distinct cortical areas exist dealing with various aspects of social cognition processes. In particular, the aMFC has been associated with the perception of one’s own and others’ emotional state, and with making inferences about others’ thoughts in various tasks including affect evaluation, mental state inference, and theory of mind tasks. The observed activation within the aMFC during perception of emotional laughs as compared to tickling laughter is in line with the proposed differences of social communicative functions of the respective laughter types: While tickling laughter is an unequivocal signal which has a direct impact on the listener and, therefore, imposes only moderate demands on social cognition processes, emotional laughter is an equivocal signal which may incorporate diverse meanings and, therefore, imposes higher demands on social cognition processes.

The direct comparison of taunting laughter and joyful laughter did not show significant differences in cerebral activation between these two types of emotional laughter. This observation further supports the importance of the distinction between tickling laughter and emotional laughter, whereas the valence of a specific type of emotional laughter seems to have less impact on cerebral activation.

The assumed independence of these stimulus-related effects from task-directed changes of attention was confirmed by comparable aMFC activation during explicit and implicit emotional processing. Thus, even in a situation where the listener’s attention is not explicitly focused on emotional evaluation the aMFC is activated by emotional laughter.

Our second hypothesis assumed that differential acoustical profiles of tickling and emotional laughter would be evident in differential activation of secondary auditory cortex. Confirming this assumption we found that tickling laughter showed increased activation in right hemispheric secondary acoustic regions located in the mid-STG posterior to Heschel’s gyrus. Generally, the right mid-STG has been shown to be sensitive to voices (Belin et al., 2002, 2000). Moreover, this region has been linked to the processing of sounds with changing spectral and temporal parameters (Riecker et al., 2002; Warren et al., 2005, 2006) and processing of higher order acoustic cues (Ethofer et al., 2006c; Grandjean et al., 2005; Wiethoff et al., 2008; Wildgruber et al., 2005). Therefore, we suggest that in the present study higher activation of mid-STG for tickling laughter most likely reflects processing of certain voice qualities characterizing tickling laughs in contrast to joyful and taunting laughs, such as increased laugh rate and large amount of voiced energy (Szameitat et al., 2009).

The observed differences in cerebral activation between the two laughter types are in accordance with evolutionary considerations: Increased activation in the mid-STG for tickling laughter is in line with far-reaching evolutionary roots of these laughs, as this area is not only well developed in social animals but is also activated when humans listen to animal sounds (Belin et al., 2007; Fecteau et al., 2004). The processing of emotional laughter, however, relies strongly on a frontomedial area, i.e. a phylogenetically younger brain region that is less developed in animals (Öngür et al., 2003). Our study therefore provides suggestive evidence that laughter, in the form of a reflex-like reaction to touch, has been adopted into human social behavior from animal behavior (Ross et al., 2009). Through the differentiation of human social interaction over time this “simple” form of laughter may have diversified to become a spectrum of different laughter variants in order to accommodate increased complexity of human social interaction.

The claim that laughter has diversified in human phylogeny is further supported by convergent evidence in the ontogenetic development of human laughter, i.e., different laughter types show different onsets during the development of a child (Bainum et al., 1984; Justin, 1932; McGhee, 1979; Sroufe and Wunsch, 1972). Critically, in line with the idea that human tickling laughter is phylogenetically old and hence closely related to the animal tickling laughter, tactile stimuli, such as tickling are one of the first laughter elicitors in children (McGhee, 1979; Sroufe and Wunsch, 1972; Washburn, 1929). However, as development progresses in children the number and type of laughter eliciting stimuli increases, whereby social stimuli become increasingly more important (McGhee, 1979; Sroufe and Wunsch, 1972). Also at the level of acoustic properties, the laughter signals become increasingly variable as children grow older (Mowrer, 1994; Nwokah et al., 1993, 1999) and is more and more affected by individual characteristics and cultural conventions (Porteous, 1988; Stern, 1985).

Considering task-directed changes of attention during perception of laughter sounds, explicit evaluation of laughter type was associated with increasing activation within a network comprising the right posterior STS, the bilateral IFG, OFC and prMFC. Involvement of the right posterior STS for explicit emotional evaluation of laughter is in line with findings on evaluation of emotional speech prosody (Ethofer et al., 2006a; Wildgruber et al., 2005, 2006, 2009). Activation of the IFG and OFC (BA 45/44/47) for explicit emotional evaluation is in line with other studies on explicit vocal emotional judgment (Ethofer et al., 2006a,b, 2009; Wildgruber et al., 2004, 2005, 2006, 2009). Accordingly, IFG activation likely reflects increased demands underlying top-down control of emotional evaluation. However, activation of right hemispheric IFG is not restricted to emotional evaluation, i.e. it has also been reported for evaluation of linguistic prosody (Wildgruber et al., 2004), discrimination of certain acoustical

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**Table 3**

<table>
<thead>
<tr>
<th>EXP−IMP</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-score (peak voxel)</th>
<th>Cluster size (voxel)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L inferior frontal gyrus pars triangularis/pars orbitalis/L Insula</td>
<td>−39</td>
<td>21</td>
<td>−9</td>
<td>4.91</td>
<td>168</td>
</tr>
<tr>
<td>R inferior frontal gyrus pars triangularis/pars orbitalis/pars opercularis</td>
<td>57</td>
<td>27</td>
<td>12</td>
<td>4.68</td>
<td>239</td>
</tr>
<tr>
<td>L ± R medial superior frontal gyrus</td>
<td>−3</td>
<td>36</td>
<td>48</td>
<td>4.42</td>
<td>94</td>
</tr>
<tr>
<td>R superior temporal gyrus/R middle temporal gyrus</td>
<td>42</td>
<td>−48</td>
<td>3</td>
<td>4.39</td>
<td>101</td>
</tr>
</tbody>
</table>

Activations thresholded at p<0.001, uncorrected with a cluster size k≥25 voxels. Coordinates refer to the MNI system. All activations significant (p<0.05, corrected for multiple comparisons across the a priori anatomical ROI (see Methods)).
parameters, such as pitch, timbre, or intensity (Auzou et al., 1995; Belin et al., 1998; Paus et al., 1997; Zatorre et al., 1994, 1992, 1999), discrimination of spatial location of sounds (Zatorre et al., 1999), and processing of visual or somatosensory stimuli (Mecklinger et al., 2000; Pardo et al., 1991) suggesting that this area is part of a multimodal network for attention and working memory involved in a variety of tasks of different domains (Mecklinger et al., 2000; Zatorre et al., 1992, 1999). Activation of right dominant IFG in the present study might reflect attentional demands such as directing attention towards emotional prosody (Belin et al., 2004), demands in working memory for voices (Rämä and Courtney, 2005) such as holding prosodic cues of the laughs online, or demands on retrieval of verbal or emotional memory (Buchanan, 2007; Schirmer and Kotz, 2006) such as the attachment of emotional labels to vocal stimuli. Finally, task-dependent activation of the prMFC during perception of laughter and speech prosody (Ethofer et al., 2009) is consistent with the assumption that the posterior part of the rostral MFC is associated to cognitive processes contributing to action monitoring and focusing of attention (Amadio and Frith, 2006). To sum up, the observed commonalities with neural networks underlying explicit emotional evaluation of speech prosody and laughter suggest that both processes are subserved by similar neural networks.

In conclusion, the observed dissociation of neural activity underlying perception of tickling laughter and emotional laughter supports the assumption that a phylogenetically old, “reflex-like” form of laughter has diversified into socially more sophisticated types of laughter. Presumably, the diversification of social communicative functions and associated acoustic structure of laughter types has been driven by changing requirements of social behavior throughout the evolutionary process.

Acknowledgments

We thank the Marie Curie Foundation and the German Research Foundation (DFG WI 2101/2-1) for financial support.

References


