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Neural correlates of the affective properties of spontaneous and volitional laughter types

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Abstract

Previous investigations of vocal expressions of emotion have identified acoustic and perceptual distinctions between expressions of different emotion categories, and between spontaneous and volitional (or acted) variants of a given category. Recent work on laughter has identified relationships between acoustic properties of laughs and their perceived affective properties (arousal and valence) that are similar across spontaneous and volitional types (Bryant & Aktipis, 2014; Lavan et al., 2016). In the current study, we explored the neural correlates of such relationships by measuring modulations of the BOLD response in the presence of itemwise variability in the subjective affective properties of spontaneous and volitional laughter. Across all laughs, and within spontaneous and volitional sets, we consistently observed linear increases in the response of bilateral auditory cortices (including Heschl's gyrus and superior temporal gyrus [STG]) associated with higher ratings of perceived arousal, valence and authenticity. Areas in the anterior medial prefrontal cortex (amPFC) showed negative linear correlations with valence and authenticity ratings across the full set of spontaneous and volitional laughs; in line with previous research (McGettigan et al., 2015; Szameitat et al., 2010), we suggest that this reflects increased engagement of these regions in response to laughter of greater social ambiguity. Strikingly, an investigation of higher-order relationships between the entire laughter set and the neural response revealed a positive quadratic profile of the BOLD response in right-dominant STG (extending onto the dorsal bank of the STS), where this region responded most strongly to laughs rated at the extremes of the authenticity scale. While previous studies claimed a role for right STG in bipolar representation of emotional valence, we instead argue that this may in fact exhibit a relatively categorical response to emotional signals, whether positive or negative.

Keywords

Laughter; Perception; affective properties; fMRI; parametric modulations; Laughter; perception; affective properties; fMRI; parametric modulations

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Introduction

Traditionally, emotional signals have been viewed as unitary in their meaning. A wealth of studies on emotion category recognition supports this view, showing that participants can reliably recognise emotional signals in different modalities, within and across cultures (Ekman & Friesen, 1971; Elfenbein & Ambady, 2002; Paulmann & Uskul, 2014; Sauter, Eisner, Ekman, & Scott, 2010; Sauter & Scott, 2007). This view may, however, be relatively simplistic: One type of vocalisation can signal a range of meanings, depending on the context in which it is produced: This is effectively exemplified by laughter (Bachorowski & Owren, 2001; Gervais & Wilson, 2005). Laughter is observed across the great apes and associated with positive emotional experience, such as during play (Provine, 2000; Ross, Owren, & Zimmermann, 2009; Scott, Lavan, Chen, & McGettigan, 2014). In humans, laughter vocalisations emerge at a very early stage in infancy, typically during tactile/tickling interactions with a caregiver (Scheiner, Hammerschmidt, Jürgens, & Zwirner, 2006), and continue to be used frequently in play and conversation contexts. Recent evidence suggests that non-human primates produce different types of laughter vocalisations for different social outcomes (e.g. during play vs. in response to others to prolong play); while some laughter reflects automatic and involuntary signalling of the positive emotional state, other types may be produced under greater volitional control (Davila-Ross, Allcock, Thomas, & Bard, 2011). Similarly, laughter in humans can occur as a consequence of intense amusement, but can also be used volitionally to communicate polite agreement (Scott et al., 2014).

Recent research on laughter perception has shown that participants can make accurate within-vocalisation judgements of the meaning of laughter signals: participants can reliably judge the authenticity of a laugh, that is whether a laugh was produced in response to genuine amusement or whether it was produced without a particular underlying emotional state (Bryant & Aktipis, 2014; Lavan, Scott, & McGettigan, 2016; McGettigan et al., 2015). A study showed that listeners from 24 different cultures could discriminate laughter produced within pairs of friends from that occurring within newly-acquainted dyads (although with only 53-67% accuracy; Bryant et al., 2016); other work has indicated that authentic voiced laughter is perceived as more positive, friendlier and more attractive compared to authentic unvoiced laughter (i.e. grunt-like or snort-like laughter; Bachorowski & Owren, 2001). These studies thus show that a wealth of nuanced affective features is encoded within a single vocalisation and can be reliably decoded by listeners.

One such affective feature, the authenticity of a vocalisation, has been the focus of several recent studies. In terms of production, neurobiological accounts propose that spontaneous laughter is under the control of an evolutionarily older midline system associated with innate vocalisations (and closely related to vocal control systems of non-human primates), while volitional laughs are controlled by regions of lateral motor cortex associated with learned vocalisations such as speech and song (Wild, Rodden, Grodd, & Ruch, 2003) As a result of the distinct systems and production mechanisms for volitional and spontaneous laughter, studies argue that there are aspects of spontaneous laughter that are unique and “hard to fake” (Bryant & Aktipis, 2014; McKeown, Sneddon, & Curran, 2015), yet apparently these can be relatively well simulated volitionally, in order to smooth social interactions (Bryant et al., 2016). According to Bryant and Aktipis (2014), human laughter behaviours thus reflect an evolutionary “arms race”: while it is important for listeners to be able to detect genuine expressions of emotion, it is also advantageous for laughers to be able to deceive a listener by producing passable laughter vocalisations (e.g. to gain group membership), presumably using newer cortical control mechanisms to simulate emotional vocalisations. In line with this argument, Lavan et al. (2016) found that variability in perceived arousal and valence in spontaneous and volitional laughter was associated with highly similar constellations of acoustic predictors. Further, two studies have measured the neural responses to different laughter types (McGettigan et al., 2015; Szameitat et al., 2010). McGettigan and colleagues directly compared passive responses to spontaneous and volitional laughs (labelled “Evoked” and “Emitted”, respectively, in the paper), finding that spontaneous sounds were associated with stronger BOLD responses in bilateral primary auditory cortex (Heschl’s gyrus) and STG. Similarly, Szameitat et al. (2010) measured passive and active responses to 3 laughter types (tickling, joy, and taunting) and identified a significant cluster showing a preferential response to tickling laughter in right STG (in a location closely corresponding to the peak in McGettigan et al., 2015) that was unmodulated by attention. Conversely, preferential responses to more socially complex laughter (volitional/”Emitted” laughter in McGettigan et al., 2015; joy and taunting laughter in Szameitat et al., 20010) were found in similar regions of anterior medial prefrontal cortex (amPFC) across the two studies. Individual contrasts additionally revealed areas including anterior insula, thalamus, anterior cingulate cortex and precuneus, leading both sets of authors to conclude that these laughter types made stronger demands on processes potentially associated with mentalizing, theory of mind, and affective evaluation.

In both of these studies, it was not established whether the activations observed in STG for spontaneous and tickling laughter types reflect the perception of the meaning of these items, or a more basic effect of their underlying acoustic properties. It has been shown that, for example, spontaneous laughter is longer in duration, less voiced, higher-pitched, and with higher spectral centre of gravity and intensity than volitional laughter, yet a matched set of acoustic variables can account for similar amounts of variability in arousal and valence (though not authenticity) for the two laughter types (Lavan et al., 2016). Thus, a preferential response to spontaneous laughs in STG may simply be a reflection of their more extreme acoustic properties. However, trying to partial out the acoustic differences between sound categories presents its own problems when investigating responses in auditory cortex – by their nature, the perceptual properties of auditory stimuli are carried by some combination of acoustic cues (Wiethoff et al., 2008). Should partialling out acoustic cues lead to a complete abolition of neural signal, this might reflect merely that the stimuli in question are sounds; more troublingly, if partialling out leads to the *preservation* of signal in auditory cortex, we cannot tell whether this is because the remaining signal is truly reflective of higher-order processing, or just the residuals of an incomplete attempt to account for acoustic properties.

To avoid conflating acoustics and affective perception through basic categorical subtraction, we can alternatively investigate how the BOLD response in temporal cortex varies with the affective perception of laughter in a more continuous fashion, by exploring the modulation of the signal by itemwise affective properties of the sounds. By measuring the neural correlates of perceived properties such as arousal and valence, we can examine whether these engage similar brain regions within each laughter type and test the “arms race” view of volitional human laughter – that is, we can assess whether affective cues can indeed be contrived volitionally to engage the same regions as similar modulations in spontaneous laughs.

The natural variability in the affective properties of laughs can also be harnessed to identify neural responses that are more reflective of categorical perception of laughter types. Previous work has shown U-shaped responses in right STS associated with the perceived intensity of positive and negative emotional prosody (Ethofer et al., 2007) and sounds varying in their pleasantness (Viinikainen, Kätsyri, & Sams, 2012), where the signal becomes greater with increasing distance from neutral. In the case of authenticity in laughter, we can probe the brain for separate linear responses to spontaneous and volitional laughs that increase with greater category representativeness (i.e. greatest for low-authenticity volitional laughs and high-authenticity spontaneous laughs), or for positive quadratic relationships with authenticity across the combined laughter types. By testing the converse models between the BOLD signal and affective ratings, we can ask for example whether regions such as the amPFC sites reported by McGettigan et al. (2015) and Szameitat et al. (2010) are signalling the “category” ambiguity of laughter (e.g. showing a greater response to items rated in the mid-range for authenticity, and thus more difficult to label as “real” or “posed”) or showing a basic monotonic sensitivity to variability in laughter’s affective properties. If the latter holds (i.e. a negative linear relationship between authenticity and BOLD in amPFC), we argue that this reflects a role for amPFC not in the basic classification of laughter types, but in the processing of its social ambiguity – that is, while both the spontaneous and volitional sounds can be recognised as laughter, the causes and meaning of volitional tokens are less clear and therefore engage additional higher-order mentalizing computations (McGettigan et al., 2015; Szameitat et al., 2010).

The current study used natural variability in spontaneous and volitional laughter samples to address three theoretical questions. First, is the behavioural evidence for the evolutionary “arms race” underpinned by overlapping neural responses to variation in the affective properties of laughter? Second, can we differentiate monotonic relationships between sound and emotional properties from higher-order sensitivities to laughter types in the auditory processing pathway (i.e. increasing responses to laughs that are clearly “real” and clearly “fake”)? Third, can we more clearly establish the basis for amPFC engagement during passive listening to laughter? We collected behavioural ratings of arousal, valence and authenticity for a set of spontaneous and volitional laughs, and used these itemwise values to explore regions showing linear and quadratic modulations of the BOLD response during passive listening to the same laughter samples. Based on our previous findings related to the acoustic predictors of affective properties of laughter (Lavan et al., 2016), we predicted that overlapping regions of bilateral Heschl’s gyrus and STG would show positive linear relationships with all three affective scales, both within and across laughter types, reflecting the close association between acoustic cues and affective perception. We did not predict that we would observe non-linear relationships in the STS, given the previous work associating this region with increased emotional valence and intensity, and that both spontaneous and volitional laughter are perceived as positively valenced. Finally, we predicted that a quadratic and negative relationship would be seen in anterior cingulate and amPFC, potentially reflecting a role for these regions in resolving categorically ambiguous percepts (where "category" is used here not in the sense of distinct categories of emotions, but rather referring to different classes of stimuli that are commonly recognized as laughter; cf (Bestelmeyer, Maurage, Rouger, Latinus, & Belin, 2014; Lavan & Lima, 2014).

Method

Here, we describe an affective ratings task used to calculate mean itemwise ratings of perceived arousal, valence and authenticity for spontaneous and volitional laughter. These were further employed to probe the modulation of the neural responses to passively heard laughter by their affective properties. The functional MRI data used in the current study were originally collected in a study comparing passive neural responses to two different types of laughter, spontaneous ("Evoked", in McGettigan et al., 2015) and volitional ("Emitted", in McGettigan et al., 2015) laughter, as well as investigating individual differences in authenticity detection. For that study, spontaneous laughs were generated by 3 female speakers in response to amusing video and audio clips, while another set of volitional laughs were produced "on demand", without any external stimulation, by the same speakers (for full details of the vocalisations, as well as the fMRI study participants, materials and procedure, please see McGettigan et al., 2015). The original study was approved by the UCL Research Ethics Committee.

Affective ratings experiment

Participants—Twenty participants (11 female; mean 22 yrs 6 mo, S.D. 2.5; range 21 – 32 years) with healthy hearing (self-reported) completed the ratings task. None of these individuals had participated in the previous fMRI study. The behavioural study was approved by the Departmental Ethics Committee at the Department of Psychology, Royal Holloway, University of London.

Design & Procedure—Each participant rated the 84 original auditory stimuli from the functional imaging experiment - 21 spontaneous laughs, 21 volitional laughs, 21 sounds of disgust (volitional), 21 unintelligible baseline (spectrally-rotated) sounds - on 7-point Likert scales of perceived arousal and valence. For arousal, participants were asked "How aroused does this sound?", with 1 being "low arousal: the sound is very drowsy and not energetic" and 7 being "high arousal: the sound is very wakeful and energetic". For valence, they were asked "How positive or negative does this sound?", with 1 being "very negative" and 7 being "very positive". For the laughter and disgust categories only, participants completed a third scale for perceived authenticity, for which they were asked "How authentic does this sound?", with 1 being "not authentic at all" and 7 being "very authentic". Each scale formed a separate block of the experiment, with the arousal and valence blocks presented first and counterbalanced across participants; the authenticity scale was always presented last, so as not to alert participants to the experimental manipulation within the laughter sounds. The stimuli were presented using Matlab (version R2007), with the Psychophysics Toolbox extension (Brainard, 1997). Stimuli were presented over headphones (Sennheiser HD201; Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) while the participant viewed a crosshair. After playback, a rating scale appeared on the screen and the participant was asked to make a selection from 1 to 7 by making a key press; in the absence of a response, the trial timed out 2.5 seconds after the appearance of the rating scale. Stimuli were presented in a fully randomized order within each block.

fMRI experiment

Participants—The participants in the functional imaging experiment (originally reported in McGettigan et al., 2015) were 21 right-handed adult speakers of English (13 females; mean age 23 years 11 months). All participants reported healthy hearing and no history of neurological incidents, nor any speech or language problems. The study was approved by the UCL Research Ethics Committee.

Data Acquisition and Preprocessing—The functional MRI data comprised two runs of 110 whole-brain echo-planar volumes collected during the auditory session of the experiment reported in McGettigan et al. (2015): Briefly, in each run of this experiment, adult participants (N = 21) passively listened to all 84 stimuli (21 of each category: spontaneous laughs, volitional laughs, disgust sounds, baseline sounds, see Design & Procedure) presented via insert earphones in a pseudo-randomised order. Whole-brain echo-planar volumes (TR = 9 s, TA = 3 s, TE = 50 ms, flip angle = 90°, 35 axial slices, 3 mm × 3 mm × 3 mm in-plane resolution) were collected using a sparse-sampling routine, with presentation of an audio stimulus occurring in the silence between acquisitions, 4.3 seconds (+500ms jitter) before the onset of the next volume. Rest Baseline trials (fixation cross on the screen no sound or task) were presented in 5 evenly spaced miniblocks, each lasting 7 TRs. For the current study, these data were preprocessed and analyzed in SPM8 (Wellcome Trust Centre for Neuroimaging, London, UK). Functional images were realigned and unwarped, co-registered with the anatomical image (HiRes MPRAGE; see McGettigan et al., 2015), normalized using parameters obtained from unified segmentation of the anatomical image, and smoothed using a Gaussian kernel of 8 mm FWHM.

Statistical analysis—For each subject, 6 first-level General Linear Models were implemented within SPM8. In the first three (Models 1-3), event onsets for spontaneous laughter, volitional laughter, disgust and baseline sounds were modeled as instantaneous and convolved with the canonical haemodynamic response function in SPM8. Six movement parameters generated during the realignment step of preprocessing were included as regressors of no interest. For the laughter conditions only, a single, first-order parametric modulator was included that described mean itemwise arousal (Model 1), valence (Model 2) or authenticity (Model 3) ratings[1]. Within these models, volitional laughter and spontaneous laughter were entered as separate regressors to compare results between the two laughter types. In the remaining models (Models 4-6), volitional and spontaneous laughter events were combined into a single onsets regressor; the models also included separate disgust and

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[1] Note that mean item-wise post-hoc ratings were used that were independent from the neuroimaging data. This was necessary due to the nature of the in-scanner task (passive listening without being made aware of the presence of volitional and spontaneous laughter). Thus, while these ratings do not reflect trial-wise perceptual evaluations of the vocalisations in the scanner, they nonetheless provide valuable estimates of the vocalisations' perceptual and affective properties. This fact is further underlined by the high interrater reliability present in the data (across all vocalisations [volitional laughter, spontaneous laughter, baseline and disgust sounds, Cronbach's alpha = .901 – .972; for spontaneous and volitional laughter only, Cronbach's alpha = .888 - .925), indicating similar and reliable patterns of affective ratings across individuals

baseline onsets regressors as before, as well as the six movement regressors of no interest. Here, parametric modulators were included with a 3rd-order polynomial expansion to allow for the exploration of both linear and quadratic effects of arousal (Model 4), valence (Model 5) and authenticity (Model 6). We included the cubic expansion of the regressors here in order to partial out higher-order contributions in the examination of quadratic effects (see (Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007).

For Models 1-3, contrast images were calculated to describe the positive linear effects of the parametric modulator on the spontaneous (Contrast 1) and volitional (Contrast 2) conditions. For Models 4-6, two contrasts were calculated describing the positive linear (Contrast 1) and quadratic (Contrast 2) effects of the parametric modulator on responses to the combined laughs. A set of second-level one-sample T-test models then explored the positive and negative effects of the modulators in a random-effects group analysis. All second-level results are presented at a voxel height threshold of $p < .005$ (uncorrected) – a cluster extent of 20 voxels (540mm^3; each voxel 3x3x3mm in volume) was applied to correct for inflated Type I errors ($p < .001$; calculated using a Monte Carlo simulation with 1000 iterations; (Slotnick, Moo, Segal, & Hart, 2003). In all results tables, we additionally highlight clusters and local peaks surviving a family-wise error corrected threshold of $p < .05$.

Plotting parametric modulations—The rfxplot toolbox in SPM8 (Gläscher, 2009) was used in order to visually explore significant linear and quadratic modulations of the BOLD responses to spontaneous, volitional and combined laughs. For the peak voxel within each significant cluster, laughter events were binned according to their mean affective rating and the mean percent signal change extracted for each bin – the toolbox was further used to fit linear and quadratic functions to each plot. It should be noted that negative % signal change values in these plots do not indicate suppression relative to the rest baseline – the y-axis values correspond to modulation of the BOLD signal relative to the mean response to laughter events.

Results

Affective ratings

Independent samples t-tests on the behavioural ratings showed that spontaneous laughs were rated significantly higher than volitional laughs on arousal ($t[40] = 10.57$, $p < .001$, Cohen's $d = 3.34$, 95% CI [1.21, 1.78]), valence ($t[40] = 9.50$, $p < .001$, Cohen's $d = 3.00$, 95% CI [0.93, 1.44]) and authenticity ($t[40] = 12.66$, $p < .001$, Cohen's $d = 4.00$, 95% CI [1.92, 2.64]). Figure 1 shows scatterplots of the mean affective ratings for each spontaneous and volitional laugh, for each pairwise combination of affective scales. Pairwise Pearson's correlations between rating scales were all positive and significant, across all laughs (two types combined) and within each laughter type - see Table 1 for details. Our previous work has reported similarly high correlations between affective scales in the perception of laughter (Lavan et al., 2016, Lavan & McGettigan, 2016), thus indicating the presence of inherent dependencies of affective features within and across different types of laughter. Given the naturally high inter-correlation of arousal, valence and authenticity in the stimuli sampled for the current study, it would be theoretically ill-motivated and practically impossible for us to make strong claims about the distinct neural correlates of any single affective property. Thus, we refrain from direct comparisons of the scales in our analyses, and in our discussion.

Importantly, although the behavioural ratings show significant differences between the laughter sets on all perceptual scales, inspection of the scatterplots (Figure 1) shows that there was an even distribution of items across all three scales (NB as all laughs were perceived as positive, values were restricted to the positive arm of the valence scale, i.e. >4). This validates our decision to explore continuous relationships between the BOLD response and laughter properties across the collapsed laughter sets.

Functional MRI

Combined spontaneous and volitional laughter

Arousal: A positive linear relationship between BOLD and itemwise ratings of arousal was found in bilateral superior temporal cortex, with peak activations in the right STG and left Heschl’s gyrus. The corresponding negative relationship revealed significant clusters in medial STS (white matter), thalamus, left inferior parietal lobule and temporal pole, and right precuneus. See Figure 2a for plots of significant activations, and Table 2 for anatomical peak voxel coordinates and statistics.

Contrasts exploring quadratic relationships between arousal ratings and the BOLD response revealed significant negative relationships in two clusters in left precuneus / post-central gyrus, and left angular gyrus. There were no significant positive relationships. These results are reported in more detail Figure 3a and Table 3 – however, given a lack of a clear motivation for exploring quadratic correlates of a unipolar scale, they will not be discussed further within this paper.

Valence: A positive linear relationship with ratings of valence was found in bilateral superior temporal cortex, with peak activations in the right STG and left Heschl’s gyrus. Clusters showing a negative relationship included left caudate nucleus, bilateral superior and middle frontal gyrus, right superior medial gyrus, left IFG (pars triangularis), left MTG and temporal pole, right precuneus and left inferior parietal lobule. See Figure 2b and Table 2.

There were significant positive quadratic relationships between valence and the BOLD response in right STG (and a cluster in left parietal white matter). There were no significant negative relationships. See Figure 3b and Table 3.

Authenticity: A positive linear relationship with ratings of authenticity was found in bilateral superior temporal cortex, with peak activations in left Heschl’s gyrus and right STG. Negative relationships were found in left thalamus and caudate nucleus, left temporal pole and IFG (par orbitalis), bilateral superior/middle frontal gyrus, bilateral superior medial gyrus, right precuneus and left inferior occipital gyrus. See Figure 2c and Table 2.

There were significant positive quadratic relationships between authenticity and the BOLD response in right STG/SMG (extending onto the dorsal bank of the STS) and left STG. There were no significant negative relationships. See Figure 3c and Table 3.

Figure 4 illustrates the overlap in activations showing positive linear and quadratic relationships with valence (4a) and authenticity ratings (4b) in right STG.

Spontaneous Laughter

Arousal: Positive correlates of arousal ratings for spontaneous laughter included bilateral STG, putamen/caudate, bilateral thalamus and cerebellum. There were no significant clusters in the contrast exploring negative correlates of arousal. See Figure 5a and Table 2.

Valence: Positive correlates of valence ratings for spontaneous laughter included bilateral STG and Heschl's gyrus (extending onto Rolandic Operculum on the left). There were no significant clusters in the contrast exploring negative correlates of valence. See Figure 5b and Table 2.

Authenticity: Positive correlates of authenticity ratings for spontaneous laughter were found in bilateral STG. There were no significant clusters in the contrast exploring negative correlates of valence. See Figure 5c and Table 2.

Volitional Laughter

Arousal: Positive correlates of arousal ratings for volitional laughter included bilateral STG and Heschl's gyrus (extending onto Rolandic Operculum on the left). There were no significant clusters in the contrast exploring negative correlates of arousal. See Figure 5a and Table 2.

Valence: Positive correlates of valence ratings for Volitional laughter included left Rolandic Operculum / STG and right STG. There were no significant clusters in the contrast exploring negative correlates of valence. See Figure 5b and Table 2.

Authenticity: Positive correlates of authenticity ratings for volitional laughter included left Rolandic Operculum / Heschl's gyrus and right STG / Heschl's gyrus. A negative linear effect was found in a single cluster on left IFG (including pars triangularis and pars orbitalis). See Figure 5c and Table 2.

Discussion

The current study used itemwise variability in the affective properties of laughter to examine and contrast the neural correlates of the perception of different types (spontaneous and volitional) within the same vocalisation category. Both within and across spontaneous and volitional laughter, we found positive linear relationships between the BOLD response in bilateral auditory cortices (including Heschl's gyrus and STG) and ratings of arousal, valence and authenticity. For the valence and authenticity scales, quadratic relationships were also identified: in both cases, a peak activation cluster in STG/STS showed greater responses to items rated at both extremes of the authenticity scale, and at the most positive arm of the valence scale. A further objective of the study was to evaluate whether amPFC responses to laughter might reflect categorical ambiguity (i.e. a difficulty in assigning a "real" vs "posed" classification) between spontaneous and volitional types; however, there was no negative quadratic relationship in mPFC, and instead negative linear trends were observed for valence and authenticity (when measured across both laughter types).

Our finding that primary and secondary auditory cortices showed a positive linear relationship with perceived arousal, valence and authenticity for both spontaneous and volitional laughs speaks to the “arms race” described by Bryant and Aktipis (2014, see also McKeown, Sneddon & Curran, 2015). Building on our previous finding that variations in affective properties of volitional and spontaneous laughter can be accounted for by similar constellations of acoustic features (Lavan et al., 2016), the current data shows that such variations also engage largely overlapping regions of auditory cortex. Our finding that this pattern holds both within and across spontaneous and volitional sets suggests that auditory cortex responds to spontaneous and volitional laughter in a continuous rather than discrete fashion. This in turn implies that producers of volitional laughter are able to successfully simulate the appropriate affective state (albeit with lower perceived levels of perceived arousal, valence and authenticity) through the modulation of acoustic cues in the voice.

Several studies have shown relationships between the emotional intensity of vocalisations and signal in right superior temporal cortex (including Heschl’s gyrus, STG and STS). A comparison of laughter and crying vocalisations with their time-reversed counterparts showed greater activation of relatively early parts of the ventral auditory processing stream bilaterally, including Heschl’s gyrus, STG and portions of the planum temporale (Sander & Scheich, 2005). Fecteau, Belin, Joanette and Armony (2007) observed stronger responses in bilateral auditory cortex (including Heschl’s gyrus, STG and STS) for non-verbal emotional vocalisations (cries and screams) compared with neutral sounds, while another study reported greater responses in the STS for angry speech compared with neutral speech (a difference that remained regardless of attention to the stimuli; Sander et al., 2005). Wiethoff et al. (2008) measured neural responses to words spoken with neutral or emotional (happy, erotic, angry, fearful) prosody, finding greater engagement of the right mid STG to sounds with emotional intonation. However, when exploring the data using linear regressions, they found that including a small constellation of 5 acoustic predictors abolished this effect. Similarly, Grandjean et al. (2005) observed that preferential responses to anger prosody in right STG/STS were insensitive to attentional modulations but overlapped with responses to the basic amplitude envelope and fundamental frequency cues to anger.

We thus suggest that variations in the diagnostic acoustic properties of spontaneous laughter, which can be partially emulated in volitional types, are coded in the responses of primary and secondary auditory cortex. However, as the “arms race” account explains, despite the capacity of laughers to simulate cues to authentic emotion in volitional laughter, it is also advantageous that listeners should be able to readily classify spontaneous and volitional laughter samples in order to avoid deception. Indeed, several previous studies have shown above-chance behavioural classification of stimuli such as those used in the current study (Bryant & Aktipis, 2014; McGettigan et al., 2015; Lavan et al., 2016; Lavan & McGettigan, 2016). Thus, the presence of sufficiently extreme acoustic cues in pitch, spectral balance, duration and intensity suggesting a lack of volitional control of the vocal system (a “pressed voice”; Szameitat, Darwin, Szameitat, Wildgruber, & Alter, 2011) may be coded within STG and communicated to other sites for evaluation/categorization of the biological and social significance of these items. Based on the existing literature measuring responses to auditory stimuli of both negative and positive valence, we predicted that this relationship between authenticity and the auditory cortical response would be monotonic throughout the temporal lobe, and titrated according to degree of emotional intensity across our set of exclusively positively-valenced laughter stimuli. However, against our predictions, we also identified U-shaped parametric relationships of both valence and authenticity with the BOLD response in downstream regions of the auditory processing pathway - inspection of parameter estimates shows these corresponded with a preferential response to laughs at the poles of the authenticity and valence scales (limited to the positive arm of the valence scale, as all laughs were rated as positive). Thus, laughs that were perceived as clearly “real” *or* clearly “fake” engaged the strongest responses in these regions of superior temporal cortex, whose location partly overlapped with those showing positive linear correlations but was focused in slightly more posterior and ventral regions of the gyrus and the dorsal bank of the STS. This non-linear response profile was observed bilaterally (but strongly right-dominant) for authenticity, and in the right hemisphere only for valence. The dorsal bank of the STS forms the focus of regions in the brain showing a preferential response to human voices, when compared with animal calls and environmental sounds (the Temporal Voice Areas, TVAs; (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000). Similarly, the STS has been associated with the processing of socially meaningful stimuli from the auditory and visual domain, interpreting the communicative function and significance of a stimulus (Redcay. 2008). In line with this, differential responses in the voice-selective areas of STS have been reported to communicative (laughter, speech) and non-communicative (coughs, sneezes) vocal signals (Shultz, Vouloumanos & Pelphrey, 2012). From our data, these sites appear to code a higher-order representation of the heard stimuli in terms of their perceived meaning, with relatively less activation for those laughs falling in the middle of the authenticity scale, and thus between ‘types’. This aligns interestingly with work on valence in emotional vocalisations; Ethofer et al., (2006) observed responses in STS to positive (happy) and negative (anger) prosody in spoken words that became larger with increasing distance from neutral intonation. Although the authors do not report a non-linear effect, the plots of parameter estimates in the paper shows that this region of STS exhibited a U-shaped function characteristic of a positive quadratic effect (Ethofer et al., 2006). A positive quadratic response was also reported for activation in “auditory cortex” (no more specific location given, though the peak voxels lie in right STG and left STS) in a study of valence in a range of sounds (human, animal, environmental, musical; Viinikainen et al., 2012).

Viinikainen and colleagues (2012) discuss the challenges of interpreting U-shaped responses to stimulus valence, which is often entangled with stimulus salience. They define salience as “the capability of stimuli to draw attentional resources, either because of their relevance to behavior in a given context […] or because of their novelty” (p. 2302). In support of a salience account, they point to studies investigating activation of the amygdala, which has shown U-shaped responses to face trustworthiness and attractiveness (Liang, Zebrowitz, & Zhang, 2010; Said, Baron, & Todorov, 2009; Winston et al., 2007). Our study sheds light on this issue within the context of emotional vocalisations and the STG/STS - we report a U-shaped response to laughter authenticity, but for a set of sounds whose valence ratings all fall within the positive arm of the scale. Thus, we might argue that valence *per se* is not what is being coded within these sites in STG/STS, but rather the salience and biological meaning of laughter samples that are perceived as unambiguously “real” or “fake”.

One of the aims of the current study was to further understand the role of anterior medial prefrontal cortex (amPFC) in the perception of spontaneous and volitional laughter. In the original paper describing these fMRI data, we found an increased response in amPFC (including superior medial gyrus and parts of the anterior cingulate cortex) in response to volitional (“Emitted”) laughs, which we attributed to the engagement of mentalizing processes to resolve the social-emotional ambiguity of these vocalisations (e.g. to attribute a mental state or motivation to a speaker producing clearly “fake” laughter; McGettigan et al., 2015). However, it was also possible that this response might have reflected ambiguity in relation to the classification of the two laughter types – in a study measuring the neural responses to auditory morphs between anger and fear vocalisations, Bestelmeyer et al. (2014) reported an inverted U-shape profile of the BOLD response in the mid-cingulate cortex and medial superior frontal gyrus that likely reflected increased responses to morphs that were ambiguous in terms of their emotion category (Lavan & Lima, 2014). If our original finding was related to a form of categorical ambiguity, we would expect a peak in the response of amPFC sites for items rated in the mid-range of the authenticity scale. However, if the response rather reflects the *social* ambiguity of the items, we would expect to see a linear decrease in amPFC activations with increased perceived authenticity: indeed, this is what we observed in the current analyses. Thus, when a listener is presented with laughter that is clearly perceived as posed, the amPFC is engaged in order to resolve the cause of this behavior. In line with this interpretation, a recent study (Skerry & Saxe, 2014) demonstrated that dorsal and middle regions of mPFC showed classification of emotional valence that generalized across both perceptual cues (facial expressions) and situational contexts that allowed the emotions to be inferred (with later work showing that representations in mPFC are not reducible to basic indices of arousal/valence; Skerry & Saxe, 2015) – this study, like ours, suggests a role for mPFC in abstracted and higher-order resolution of the meaning of emotional cues and their causes, rather than categorical or affective labeling in terms of authenticity (“real” versus “posed”).

Conclusion

We show commonality of auditory cortical sites modulated by acoustic cues to laughter authenticity, arousal and valence, for both spontaneous and volitional laughter types. However, an independent quadratic relationship with authenticity in STG/STS suggests an abstraction of acoustic cues to code the salience of vocalisations (i.e. “real” or “fake”) as information is passed along the ventral auditory processing stream. Finally, by demonstrating a continuous negative linear relationship between signal in amPFC and the perceived authenticity of laughter, we argue that this region is engaged in the processing of social ambiguity (rather than that related to low-level perceptual or categorical properties) in the processing of spontaneous and volitional laughter types. Our results are in line with the “arms race” account of laughter behaviour in human evolution - common engagement of auditory cortex by emotional variations in spontaneous and volitional laughter supports the behavioural and acoustic evidence that speakers can simulate affective vocal information voluntarily, while our findings in STS and aMPFC show that even during passive listening the human brain is sensitive to the meanings of laughter signals.

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Highlights

- We probed modulation of BOLD by itemwise perceptual qualities of laughter
- Auditory cortices responded more to higher arousal, valence, and authenticity
- Right STS was most active for items at the extremes of the authenticity scale
- Anterior medial prefrontal cortex responded most strongly to low authenticity items
- We suggest rSTS is sensitive to laughter salience, and amPFC to social ambiguity

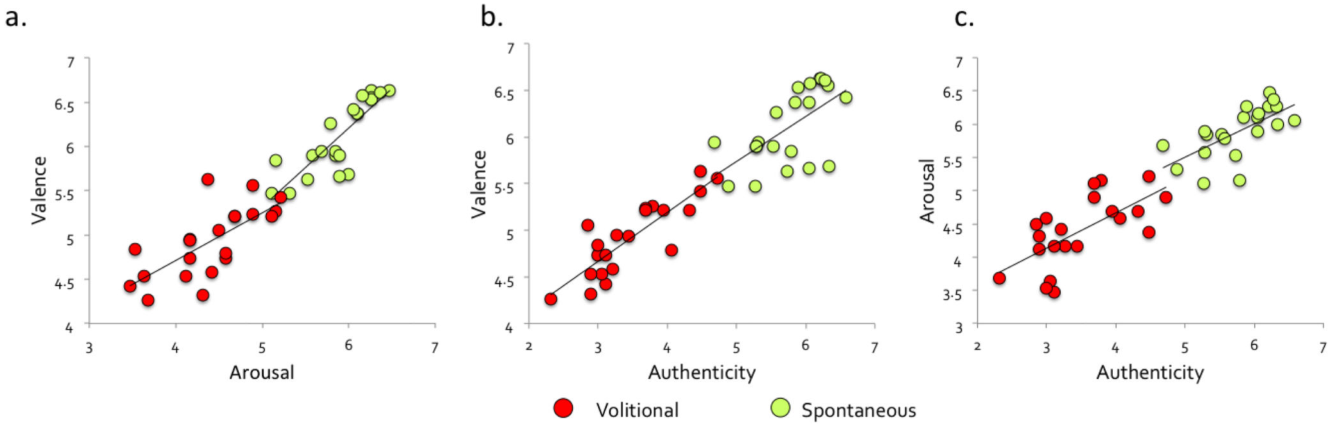

Figure 1.

a-c. Scatterplots showing the relationships between ratings of arousal, valence and authenticity for spontaneous and volitional laughs (including within-set linear trendlines).

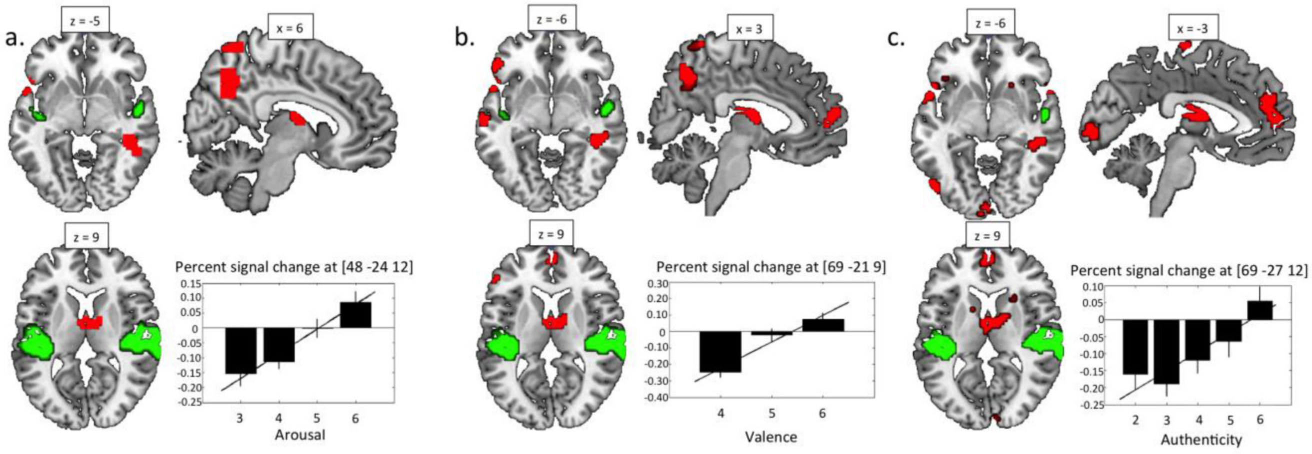

Figure 2.

Regions showing significant positive (green) and negative (red) linear relationships between the BOLD response and affective properties of laughter, across all spontaneous and volitional laughs, for a) arousal, b) valence, c) authenticity. Results are shown at a voxel height threshold of $p < .005$ (uncorrected), and a corrected cluster threshold of $p < .001$ (Slotnick et al., 2003). Bar plots show the linear trend between affective ratings and percent signal change in the peak STG voxels.

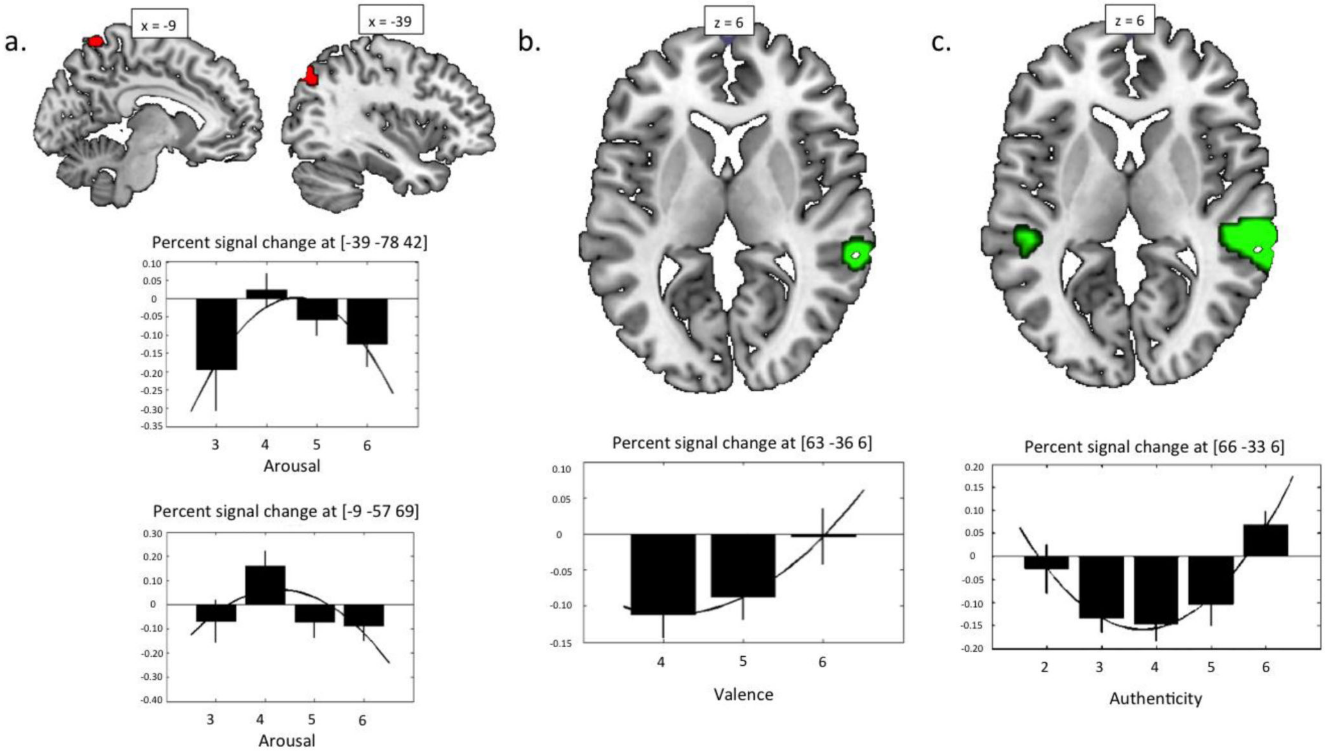

Figure 3.

Regions showing significant quadratic relationships between the BOLD response and affective properties of laughter, across all spontaneous and volitional laughs, for a) arousal, b) valence, c) authenticity. Results are shown at a voxel height threshold of $p < .005$ (uncorrected), and a corrected cluster threshold of $p < .001$ (Slotnick et al., 2003). Bar plots show the quadratic trends between affective ratings and percent signal change in the peak voxels for each analysis.

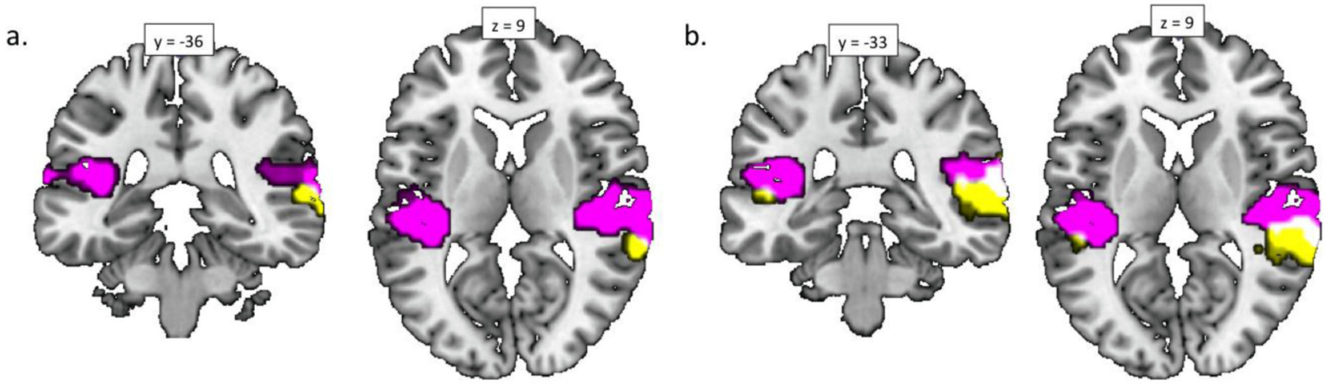

Figure 4.

Regions showing positive linear (magenta) and positive quadratic (yellow) trends in the correlation of the BOLD signal with a) valence ratings and b) authenticity ratings. Regions in white indicate overlap of the two effects. Results are shown at a voxel height threshold of p < .005 (uncorrected), and a corrected cluster threshold of p < .001 (Slotnick et al., 2003).

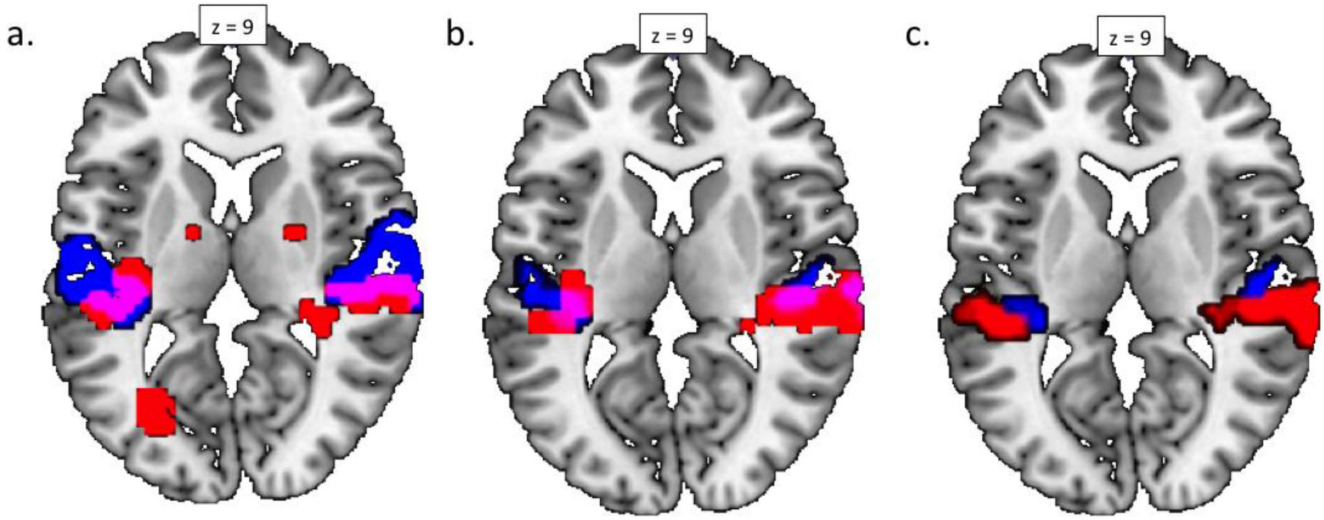

Figure 5.

Regions showing significant positive linear relationships between the BOLD response and affective properties of spontaneous (red) and volitional (blue) laughter, for a) arousal, b) valence, c) authenticity. Overlap is shown in magenta. Results are shown at a voxel height threshold of p < .005 (uncorrected), and a corrected cluster threshold of p < .001 (Slotnick et al., 2003).

Table 1

Pearson's correlation coefficients and significance estimates for pairwise correlations between affective rating scales.

Group		Arousal	Valence	Authenticity
All laughter	Arousal	-	.928**	.920**
	Valence	.928**	-	.927**
	Authenticity	.920**	.927**	-
Spontaneous laughter	Arousal	-	.841**	.663*
	Valence	.841**	-	.604*
	Authenticity	.663*	.604*	-
Volitional laughter	Arousal	-	.701**	.662*
	Valence	.701**	-	.850**
	Authenticity	.662*	.850**	-

*p < .01, **p < .001

Table 2

Results of contrasts exploring linear modulations of the BOLD signal by affective properties of both spontaneous and volitional laughter (combined) as well as split into spontaneous and volitional laughter. All results are reported at a voxel height threshold of p < .005 (uncorrected), and a corrected cluster threshold of p < .001 (Slotnick et al., 2003). Coordinates are given in Montreal Neurological Institute (MNI) stereotactic space. * Indicates a cluster or local peak that survived familywise error correction at p < .05 in SPM.

Vocalisation	**Rating Scale**	**Contrast**	**No of Voxels**	**Region(s)**	**Peak Coordinate**			**T**	**Z**
					x	**y**	**z**		
Combined volitional and spontaneous laughter	Arousal	Positive effect	660*	Right STG, insula	48	-24	12	7.36*	5.06*
			440*	Left Heschl’s gyrus, STG	-42	-24	9	7.22*	5.01*
		Negative effect	38	R STS, WM	39	-36	-9	4.89	3.92
			139	Thalamus, L caudate nucleus	0	-3	9	4.84	3.89
			37	L IPL	-42	-30	39	4.03	3.41
			22	L temporal pole	-57	12	-6	4.03	3.4
			56	R precuneus, SPL	12	-60	66	3.85	3.29
			55	R precuneus	6	-60	45	3.56	3.1
	Valence	Positive effect	593*	R STG, Heschl's gyrus	69	-21	9	7.05*	4.94*
			348*	L Heschl's gyrus, STG	-42	-24	9	6.33	4.64
		Negative effect	154	L caudate nucleus, WM	0	-3	9	5.06	4.02
			39	R SFG	21	15	66	4.78	3.86
			37	L IFG (pars. triang)	-54	39	-3	4.6	3.75
			58	R precuneus, SPL	12	-60	69	4.26	3.55
			46	R MFG	33	30	48	4.24	3.54
			21	L temporal pole	-57	15	-3	3.95	3.35
			25	L IPL	-42	-30	39	3.94	3.35
			28	R STS, WM	42	-39	-6	3.93	3.35
			28	L SFG, MFG	-24	0	63	3.67	3.17
			23	L MTG	-66	-12	-12	3.51	3.06
			37	R SMedG	3	60	12	3.5	3.06
			52	R precuneus	6	-60	45	3.45	3.02
	Authenticity	Positive effect	292*	L Heschl's gyrus, STG	-42	-24	9	6.62*	4.76*
			496*	R STG, Heschl's gyrus	69	-27	12	6.50*	4.71*
		Negative effect	41	R frontal WM	24	21	3	5.34	4.16
			268*	L thalamus, caudate nucleus, WM	-3	-6	12	5.04	4
			73	L temporal pole, L IFG (pars. orbitalis)	-57	12	-6	5.01	3.98
			21	L IOG	-51	-75	-9	4.77	3.85
			42	R SFG	21	12	66	4.49	3.69
			35	R IFG (pars. triang,), R MFG	-51	36	21	4.41	3.65
			98	R precuneus, SPL	12	-60	69	4.36	3.61

Vocalisation	**Rating Scale**	**Contrast**	**No of Voxels**	**Region(s)**	**Peak Coordinate**			**T**	**Z**
					x	**y**	**z**		
			35	R MFG	33	30	48	4.18	3.5
			25	R temporal pole	54	18	-12	4.03	3.41
			47	L calcarine gyrus	0	-93	0	3.99	3.38
			21	L paracentral lobule	-3	-18	69	3.9	3.32
			33	R precuneus	9	-54	42	3.89	3.32
			26	R temporal WM	45	-33	-9	3.87	3.31
			23	L thalamus, WM	-24	-24	21	3.77	3.24
			99	R SMedG, L SMedG	3	60	15	3.71	3.2
			22	R SMedG, SFG	18	69	12	3.38	2.97
Spontaneous laughter	Arousal	Positive effect	148	L STG, insula	-45	-15	-3	6.13	4.55
			22	R/L cerebellum	-6	-45	-24	5.71	4.35
			45	L occipital WM	-30	-72	6	5.5	4.24
			149	R Heschl's gyrus, STG, WM	30	-30	15	5.27	4.13
			30	R putamen, caudate nucleus, WM	24	-6	15	4.15	3.48
			23	Left thalamus, WM	-18	3	15	4.15	3.48
			30	Right thalamus, basal forebrain	0	6	-3	4.12	3.47
	Valence	Positive effect	303*	R STG, L Heschl's gyrus, temporal WM	45	-27	9	5.08	4.02
			140	L Heschl's gyrus, L STG, L Rolandic Operculum	-36	-21	9	4.61	3.76
			36	R parietal WM	33	-54	33	4.28	3.56
	Authenticity	Positive effect	283*	R STG, R temporal WM	63	-24	9	5.86	4.42
			116	L STG	-51	-33	9	4.9	3.93
Volitional	Arousal	Positive effect	489*	R STG, R Heschl's gyrus	60	-6	3	6.17	4.57
			356*	L Rolandic Operculum, L STG	-39	-33	15	5.79	4.39
			22	R frontal WM	18	36	-9	4.22	3.53
	Valence	Positive effect	188*	L Rolandic Operculum, L STG	-36	-30	15	6.66*	4.78*
			207*	R STG	57	-9	0	4.94	3.95
	Authenticity	Positive effect	63	L Rolandic Operculum, L Heschl's gyrus	-36	-30	15	6	4.49
			39	R STG, R Heschl's gyrus	57	-9	0	3.73	3.21
		Negative effect	22	L IFG (pars. triang., pars. orbitalis)	-36	30	0	3.24	2.87

Table 3

Results of contrasts exploring quadratic modulations of the BOLD signal by affective properties of both spontaneous and volitional laughter (combined). All results are reported at a voxel height threshold of p < .005 (uncorrected), and a corrected cluster threshold of p < .001 (Slotnick et al., 2003). Coordinates are given in Montreal Neurological Institute (MNI) stereotactic space. * Indicates a cluster or local peak that survived familywise error correction at p < .05 in SPM.

Rating Scale	Contrast	No of Voxels	Region(s)	Peak Coordinate			T	Z
				x	y	z		
Arousal	Negative effect	24	L precuneus, postcentral gyrus	-9	-57	69	3.69	3.19
		29	L angular gyrus	-39	-78	42	3.30	2.91
Valence	Positive effect	28	L parietal, WM	36	-51	30	5.05	4.01
		51	R STG	63	-36	6	4.22	3.53
Authenticity	Positive effect	432*	R STG, R SMG	66	-33	6	6.60*	4.76*
		20	L STG	-48	-33	6	3.70	3.19