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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.

1. 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 and Friesen, 1971; Elfenbein and Ambady, 2002; Paulmann and Uskul, 2014; Sauter et al., 2010; Sauter and 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 and Owren, 2001; Gervais and Wilson, 2005). Laughter is observed across the great apes and associated with positive emotional experience, such as during play (Provine, 2000; Ross et al., 2009; Scott et al., 2014). In humans, laughter vocalisations emerge at a very early stage in infancy, typically during tactile/tickling interactions with a caregiver (Scheiner et al., 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 et al., 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 and Aktipis, 2014; Lavan et al., 2016;

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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 and 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 et al., 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 unique ands of (Bryant and Aktipis, 2014; McKeown et al., 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 (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 et al., 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