The social life of laughter

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Laughter is often considered to be the product of humour. However, laughter is a social emotion, occurring most often in interactions, where it is associated with bonding, agreement, affection, and emotional regulation. Laughter is underpinned by complex neural systems, allowing it to be used flexibly. In humans and chimpanzees, social (voluntary) laughter is distinctly different from evoked (involuntary) laughter, a distinction which is also seen in brain imaging studies of laughter.

When do we laugh, and why?

Human beings are immersed in laughter: it is a pervasive non-verbal expression of emotion [1,2], which is universally recognised [3], and results from spasms of diaphragm and the intercostal muscles in the chest walls [4] (Box 1). Laughter is mediated strongly by social context: we are 30-fold more likely to laugh if we are with someone else than if we are on our own [1,2], and we laugh most if we can see and hear someone (even if this is via a computer) compared to voice or text interactions [5]. Laughter is also highly behaviourally contagious, and can occur when primed solely by another's laughter [2]. Observational studies have shown that laughter is commonly found in conversations, where it occurs at the rate of ~5 laughs per 10 minutes of conversation [6]. Strikingly, this is a much higher rate than the amount of laughter that people self-report [6]. Furthermore, if we are asked about when we laugh, we report that we laugh at jokes and humour [1,2]; however, observational studies show that not only does most laughter occur in conversations, but within those conversations most laughter is associated with statements and comments rather than with jokes [1,2,6]. Furthermore, in conversation, the person who laughs most frequently is the person who has just spoken, indicating that laughter is frequently not a reaction to someone else's utterance [2,6]. Much conversational laughter, therefore, is a voluntary, communicative act. For example, conversational laughter in both spoken and signed conversations is often timed to occur at the end of utterances [1]: this commonality across modalities underlines the voluntary aspect of some laughter because (at least in theory) a person could simultaneously sign and laugh if she wished to.

Consistent with this emphasis on the social roles of laughter, researchers have suggested that there are two different kinds of laughter, and that these are differentiated by how they are elicited: the laughter can be either driven by outside events (reactive, involuntary laughter) or be associated with a more voluntary communicative act – in other words, more controlled, deliberate laughter [7]. This has been overtly compared to the distinction between spontaneous and controlled smiling [7]. Work with chimpanzees has revealed a similar distinction between laughter which is generated in reaction to being tickled versus laughter which is produced during play (with the aim of making play last longer [8]).

Neural systems involved in the perception and production of laughter

The neural control of vocalization in humans is considered to involve two cortical systems acting on midbrain and brainstem motor structures, where lateral premotor and motor sites control the production of learned vocalizations such as speech and song, and a midline system involving the anterior cingulate and supplementary motor area that is associated with the production of involuntary vocalizations, such as expressions of emotion [9]. Within this framework of voluntary and involuntary vocalizations, Wild *et al.* [10] propose a model of laughter production, largely based on studies of pathological laughter, in which they identify a coordinating centre for laughter in the brainstem comprising the periaqueductal grey (PAG) and the upper reticular formation in the control of changes in facial expressions, respiration, and vocalization. These structures are proposed to receive excitatory inputs from cortical sites in the basal temporal and frontal lobes, as well as from structures in the limbic system including the hypothalamus and basal ganglia. In this case the lateral premotor cortices are implicated not in the basic production of laughter but rather in the suppression and regulation of spontaneous laughter vocalizations. Further studies will be able to determine the extent to which the PAG is involved in laughter because of its affective role, or because of the importance of the PAG in the production of vocal behaviour more widely. Furthermore, establishing the role of the lateral speech motor areas in conversational laughter, in addition to the suppression of laughter, will be important to determine the extent to which conversational laughter is part of a more voluntary vocalization system or whether laughter is always driven by midline neural systems. For example, a recent neuroimaging study [11] found that the voluntary suppression of laughter during tickling involved greater blood oxygen level-dependent (BOLD) responses in lateral sensorimotor cortex compared with when the participants were free to laugh when tickled (and when they voluntarily produced laughter without tactile stimulation). This same study [11] found that a key difference between voluntary and (relatively)

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Keywords: emotion; voice; conversation; laughter; motor control.

1364-6613/
 http://dx.doi.org/10.1016/j.tics.2014.09.002

Box 1. Metabolic breathing, speaking, and laughing

Both speaking and laughing require distinctly different control of the intercostal muscles, seen in the lower panel of Figure I as changes in chest wall movements, compared to the profile of metabolic breathing. Laughter is characterized by very rapid contractions of the intercostal muscles, resulting in large exhalations followed by individual bursts of laughter: the spectral modulation of laughter by supra-laryngeal structures is minimal. Speech shows a fine pattern of intercostal muscle movements, which are used to maintain constant sub-glottal pressure at the larynx and to provide pitch and rhythm to the speech. Unlike laughter, speech also shows considerable spectral complexity, reflecting movements of the supra-laryngeal articulators.

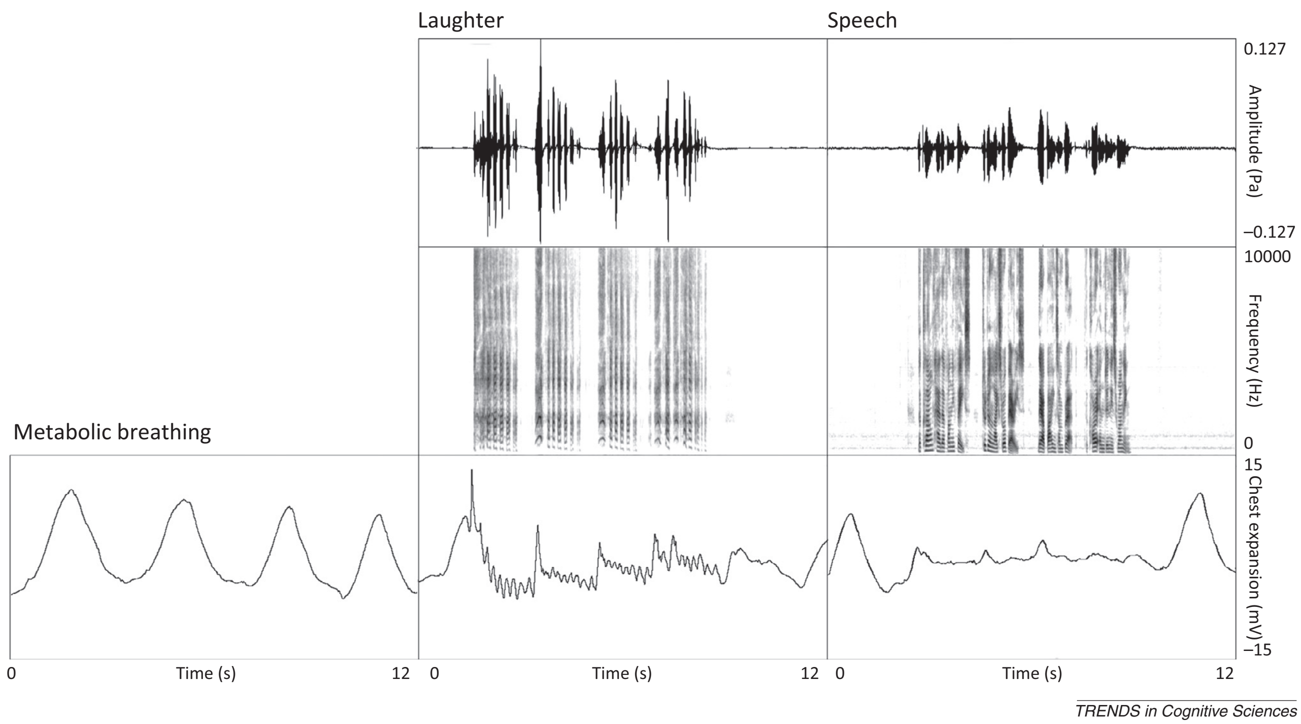

Figure I. Metabolic breathing, speaking, and laughing. The upper panel shows oscillograms for speech and laughter, the middle panel shows spectrograms for laughter and speech, and the lower panel shows chest expansion dynamics for metabolic breathing, laughing, and speaking. The timescale on the *x* axis is the same for each (breathing, laughing, and speaking).

involuntary laughter was a greater engagement of the hypothalamus during tickling laughter (compared with voluntary or suppressed laughter). It also demonstrated a correlation between activation in the PAG with the frequency of laughter episodes during tickling.

Studies of the neural correlates of laughter perception have identified sensitivities to the social significance of laughter signals. In a study of passive listening to emotional vocalizations [12], sites on the lateral premotor and primary motor cortices showed a correlation with valence, being greater to positive sounds (laughter and cheers of triumph) and lower for negative sounds (screams of fear and expressions of disgust). This could reflect the contagiousness of laughter and the greater tendency for positive vocalizations and associated facial movements to occur in the context of social groups. However, more recent work [13] showed that direct comparisons of the neural responses to voluntary and involuntary laughter recordings gave no difference in motor cortex activation. Instead, the degree of engagement of sensorimotor cortices when listening to both types of laughter was related to individual differences in the accuracy of the participants in classifying laughs as voluntary or involuntary, and as 'posed' or 'real', respectively. This could be evidence that the listener engages in some level of sensorimotor simulation as a mechanism for evaluating the social meaning of heard vocalizations, rather than exhibiting a basic sound-to-action response. In the same study, we observed preferential responses to involuntary laughter in bilateral auditory cortex, whereas responses to voluntary laughs were greater in ventromedial prefrontal cortex. This profile of auditory cortex engagement suggests that, on the one hand, there are acoustic hallmarks that automatically register the presence of intense, 'real' laughter in the brain of the listener. On the other hand, the absence or reduced prominence of such cues in voluntary laughter engages mentalizing strategies in medial prefrontal cortex to support the interpretation of why the laughter has been produced, and what it means. Figure 1 summarizes the key sites identified in studies of the production and perception of laughter.

Taking laughter seriously

Laughter is more than a positive emotional expression: its social use may extend to the management of affective states within interactions. Laughter is one of the positive emotional expressions which are expressly linked to a physiological reduction in the stressful reactions to negative emotions (e.g., fear, anger, disgust), in a way which

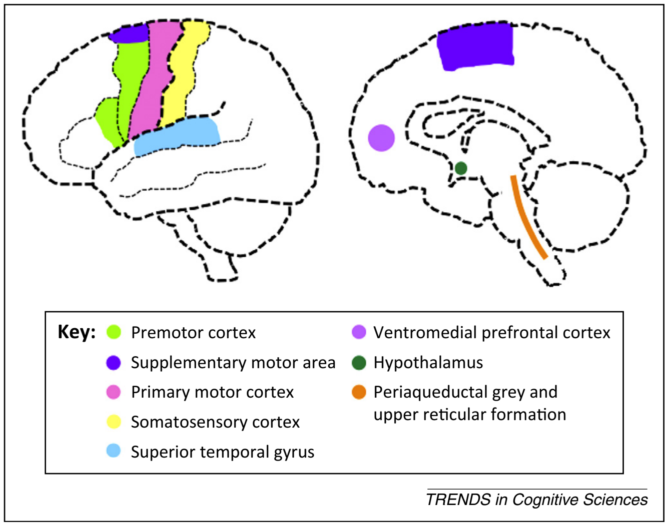

Figure 1. Voluntary and involuntary laughter in the brain. The coordination of human laughter involves the periaqueductal grey and the reticular formation, with inputs from cortex, the basal ganglia, and the hypothalamus [10]. The hypothalamus is more active during reactive laughter than during voluntary laughter [11]. Motor and premotor cortices are involved in the inhibition of the brainstem laughter centres and are more active when suppressing laughter than when producing it [11]. Laughter perception involves the premotor cortex and the supplementary motor area (SMA) [12], whereas auditory and mentalizing regions show differential engagement by involuntary and voluntary laughter [13].

may be more effective than other ways of managing negative emotions (e.g., suppression) [14,15]. Positive emotional expressions have been associated with the down-regulation of negative emotions in conversations between couples [14,15]. Couples who reported the highest levels of marital satisfaction also showed the most skilful use of positive affect (e.g., laughter) to regulate negative emotions during a difficult conversation [15]. Laughter is therefore not simply a common emotional vocalization, which we often use (not necessarily knowingly) to establish and maintain social bonds [1,2]. Laughter may also simultaneously function as an essential behaviour for helping to 'de-escalate' negative emotional experience, with a positive role in both the short-term affective state of the interaction and in the longer-term state of relationships. Understanding the behavioural and neurobiological bases of laughter will mean more than thinking about jokes. It could provide a vital link between human language, relationships, and emotional states.

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