Evolution and Human Behavior 35 (2014) 327–335

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

The animal nature of spontaneous human laughter

Gregory A. Bryant [a,b,*], C. Athena Aktipis [c,d]

[a] Department of Communication Studies, University of California, Los Angeles
[b] Center for Behavior, Evolution, and Culture, University of California, Los Angeles
[c] Center for Evolution and Cancer, University of California, San Francisco
[d] Department of Psychology, University of Arizona

ARTICLE INFO

Article history:
Initial receipt 25 March 2013
Final revision received 21 March 2014

Keywords:
Laughter
Speech
Emotional vocalizations
Communication

ABSTRACT

Laughter is a universally produced vocal signal that plays an important role in human social interaction. Researchers have distinguished between spontaneous and volitional laughter, but no empirical work has explored possible acoustic and perceptual differences. If spontaneous laughter is an honest signal of cooperative intent (e.g., derived from play breathing patterns), then the ability to mimic these sounds volitionally could have shaped perceptual systems to be attuned to aspects of spontaneous laughs that are harder to fake—features associated with phylogenetically older vocal control mechanisms. We extracted spontaneous laughs from conversations between friends and volitional laughs elicited by instruction without other provocation. In three perception experiments we found that, 1) participants could distinguish between spontaneous and volitional laughter, 2) when laugh speed was increased (duration decreased 33% and pitch held constant), all laughs were judged as more "real," with judgment accuracy increasing for spontaneous laughter and decreasing for volitional laughter, and 3) when the laughs were slowed down (duration increased 260% and pitch altered proportionally), participants could not distinguish spontaneous laughs from nonhuman vocalizations but could identify volitional laughs as human-made. These findings and acoustic data suggest that spontaneous and volitional laughs are produced by different vocal systems, and that spontaneous laughter might share features with nonhuman animal vocalizations that volitional laughter does not.

1. Introduction

Laughter is a fundamental communicative signal in humans—it is universally produced and recognizable, ubiquitous across all contexts of social interaction, and reliably developing as early as four months (Sroufe & Wunsch, 1972) with no auditory input required (Eibl-Eibesfeldt, 1970; Makagon, Funayama, & Owren, 2008). Human laughter is likely homologous to play vocalizations associated with the open mouth display in a number of primate species (van Hooff, 1972; Provine, 2000; Davila-Ross, Owren, & Zimmermann, 2009; Vettin & Todt, 2005), and analogous to related vocal signals in other social species, such as rats (Panksepp & Burgdorf, 2003) and dogs (Simonet, 2004). Provine (2000) described laughter as evolved from labored breathing during physical play. Based on comparative acoustic data on laugh-like vocalizations (play vocalizations induced by tickling) across several ape species, Davila-Ross et al. (2009) estimated that human laughter was derived from an eggressive (i.e., produced through exhalation only) play signal in the common ancestor. The species-specific modifications of this vocal behavior might have been shaped by selection beginning 5 Ma, prior to the emergence of modern human speech (see also Gervais & Wilson, 2005). Many vocalizations in the human repertoire predate speech and exist today through evolutionarily modified vocal production systems widely shared with other species (Fitch, 2006).

Some researchers have described a difference between: 1) emotionally-driven involuntary (i.e., spontaneous) laughter, and 2) volitional, non-emotional, articulated laughter (e.g., Keltner & Bonanno, 1997; Ruch & Ekman, 2001; Gervais & Wilson, 2005). Studies suggest that these laugh types depend on neurally dissociable production systems (Jurgens, 2002; Wild, Rodden, Grodd, & Ruch, 2003), but no research exists, to our knowledge, on the ability of individuals to distinguish between spontaneous and volitional laughter. Further, Gervais and Wilson (2005) noted that researchers examining laughter in natural contexts often fail to make the distinction between spontaneous and volitional forms. Provine (2012) informally explored the voluntary nature of various nonverbal behaviors (e.g., smiles, coughs, yawns), and found that the production of a laugh took over twice as long to produce (2.1 s) than a simple spoken "ha ha" (0.9 s). Spontaneous laughter is subject to neuromuscular constraints, which can be demonstrated quite readily through simple attempts to produce unnatural variants incorporating, for example, alternating vowel sounds, or extreme speed changes (Provine, 2000).

Laughter is a largely stereotyped vocalization, explaining its highly identifiable sound (Provine & Yong, 1991), but the sound characteristics are quite variable within and between individuals, and within

* Corresponding author. Department of Communication Studies, Center for Behavior, Evolution, and Culture, University of California, Los Angeles, 2303 Rolfe Hall, Los Angeles, CA 90095-1563. Tel.: +1 310 825 5984.
E-mail address: gabryant@ucla.edu (G.A. Bryant).

http://dx.doi.org/10.1016/j.evolhumbehav.2014.03.003
1090-5138/

social contexts (Bachorowski, Smoski, & Owren, 2001; Vettin & Todt, 2004). Few studies have directly examined relationships between specific acoustic properties and perceptual judgments. There is evidence that relationships between acoustic features and emotional judgments are similar across laughter and speech (Szameitat et al., 2009). Bachorowski and Owren (2001) found that voiced laughs (i.e., containing tonal information) were judged as being friendlier and more positive, compared to unvoiced laughs. Other studies have shown the importance of variability in pitch and rhythm for positive ratings (Kipper & Todt, 2001; 2003). Researchers have explored many aspects of laughter but are only beginning to understand how acoustic structure might reveal its evolutionary history and functions in modern humans.

1.1. The function of laughter and the signaling arms race

Across species, laugh-like vocalizations appear to signal positive affect and affiliation (Davila-Ross et al., 2009), and social laughter in humans could be associated with endorphin release thought to promote social bonding (Dunbar et al., 2012). Laughing might also be a reliable signal that the producer of the vocalization is unlikely to attack. In humans, laughter is known to trigger cataplexy, a sudden decrease in muscle strength. The feeling of being "weak with laughter" is likely due to increases in motor inhibition as measured by a reduction in the amplitude of reflexes during bouts of laughing (Overeem, Lammers, & van Dijk, 1999). If spontaneous laughter (but not volitional laughter) leads to muscle weakness, this could be a vital distinction between the signals.

Assuming that spontaneous laughter serves important functions in signaling positive affect and cooperative intent, we should expect selection for strategic and/or deceptive uses of volitional laughter. This, in turn, should lead to subsequent selection on perceivers to distinguish between laugh vocalizations that are emotionally driven versus those that are produced in a more deliberate manner. A co-evolutionary arms race (Krebs & Dawkins, 1984) thus ensues between production systems making volitional laughs sound more "real" and perceptual systems fine tuning distinctions between laugh types. The result would be a dynamic in which perceivers' accuracy was limited by the ability of producers to generate "real" sounding laughs. Perceivers should focus their sensitivity on features of laughs that are most difficult to emulate with the volitional speech system. The current experiments allowed us to investigate the abilities of perceivers to discriminate between spontaneous and volitional laughs as well as the acoustic features that are associated with these judgments.

1.2. The physiology of spontaneous laughter is distinct from speech

Laughing is characterized by tightly coordinated action between respiratory and laryngeal musculature (Citardi, Yanagisawa, & Estill, 1996; Luschei, Ramig, Finnegan, Bakker, & Smith, 2006) and typically contains a series of rapidly produced calls that make up a bout. Speech production, on the other hand, involves specialized fine-motor control of supralaryngeal articulators that phylogenetically older vocalizations such as laughter and crying do not necessarily incorporate (Ruch & Ekman, 2001; Szameitat, Darwin, Wildgruber, Alter, & Szameitat, 2011). The evolutionary innovation of speech enabled the volitional articulation of calls formally under the exclusive control of a phylogenetically conserved, emotional vocal production system. Emotional signals such as laughs and cries could thus be produced without the previously contingent emotional triggers in place. As described above, the ability to produce "fake" laughs could lead to a co-evolutionary arms race with mutual selection pressures on senders and receivers in the fine-tuning of the production and perception of the signals (Krebs & Dawkins, 1984). Perceivers would be under strong selection pressure to focus their discrimination abilities on those features of spontaneous laughs that are hardest to mimic using the speech system.

One unique production feature in spontaneous laughter is the rapid oscillation (~5 Hz) in the adduction cycling rate carried out by intrinsic laryngeal muscles (Luschei et al., 2006). This oscillation rate (distinct from vocal fold vibration rate) is thought to represent the maximal capability of these muscles—a limiting factor in laugh call frequency (Titze, Finnegan, Laukkanen, Fuja, & Hoffman, 2008). Rapid rhythmic laryngeal activity gives laughter its signature call structure. Specifically, thyroarytenoid and lateral cricoarytenoid activity (laryngeal adductors) has been shown to be directly associated with voiced laugh calls (Luschei et al., 2006), and elicited by the periaqueductal (PAG) region that is associated with emotional vocalizations in most mammals (Fitch, 2006). If this laryngeal control mechanism, in concert with respiratory processes, is unique to spontaneous laughter production and not fully shared by the speech production system, we might expect that perceivers would be particularly attuned to acoustic properties of laughs that are associated with rapid laryngeal activity.

Spontaneous laughs are at least partially under control of the vagal system, as most intrinsic laryngeal muscles are innervated by the recurrent laryngeal nerve which descends from the vagus nerve (Ludlow, 2013). The vagus nerve originates from the medulla and innervates the face, esophagus, larynx and many other muscles involved in vocal production. The evolution of the myelinated vagus is thought to play an important role in regulating social engagement in mammals, as well as the coordination of breathing with vocalizing (e.g., Porges, 2001), making it a potential candidate for a number of physiological and socioemotional processes associated with spontaneous laughter. It is possible that cortically controlled speech systems evolved to mimic features of spontaneous laughter generated by vagal controlled laryngeal muscles.

Speech articulation involves the dynamic interaction between breath control, voicing, and supralaryngeal modification of source sounds. Evolved refinements of the motor control of the lips, tongue, and other physiological structures allowed for mappings between articulated sounds and linguistic structure. Airflow pressure varies during speech, and the conditions when it is relatively greatest (i.e., when glottal resistance is lowest) are quite similar to vocal tract configurations during spontaneous laughter (Citardi et al., 1996). Specifically, airflow is maximized during a vowel-like configuration with the glottis opened (i.e., no voicing), occurring during the production of the /h/ sound, breathy vowels, and certain stop consonants (e.g., /ptk/) (Stevens, 1998). These airflow features of laughter are interesting for two reasons. First, they suggest that human laughter vocalizations are designed for wide broadcast. Selection for wide broadcast would have favored vocal tract shapes that maximize output capability, so the sound of a laugh likely depended upon the sound-producing capabilities of primate vocal tract morphology. Second, if airflow underlying the power of the laughter calls was crucial, the dynamics of glottal and respiratory activity between the vowel-like calls making up a laugh (i.e., glottal adduction/abduction) are likely to be distinguishing features with acoustic consequences. The spontaneous laugh system uses this particular configuration as the central space from which the calls are produced, unlike speech that typically incorporates lower airflow, and the increased engagement of supralaryngeal articulators.

Receivers might be subject to exploitation if they are a victim of deceptive uses of volitional laughter signals. The production division between spontaneous laughter and speech raises the possibility that there are perceptible acoustic features of laughter that reliably indicate the production mechanism. For example, the speech system might not be as capable of rapid laryngeal activity as the spontaneous laughter system (Luschei et al., 2006), which could lead spontaneous laughs to be often faster (i.e., average call duration measured as number of voiced calls in a single bout divided by bout length). Spontaneous laughs might also exhibit acoustic features that are associated with less cortical involvement in laryngeal control. Voicing