

Original Article

The animal nature of spontaneous human laughter

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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.

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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

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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

onsets and offsets provide plausible cues of laryngeal musculature activity that could, in turn, give perceivers information about the controlling neural pathways. Provine (2000) noted how laughter sounds quite normal after removing the unvoiced portions between calls, but suggested that the timing between voiced segments might contain information. In this study, we explore the relative duration of the unvoiced portion of laugh calls (the intervoicing interval or IVI) between spontaneous and volitional laugh bouts.

1.3. Current study

We examined judgments of spontaneous laughs produced in natural conversations between friends and a set of deliberate, volitional laughs generated on command. We expected that participants would be able to distinguish between spontaneous and volitional laughs reflecting selection on perceivers for accurate identification of dishonest portrayals of spontaneous laughter (experiment 1). We then explored whether perceptions of these sets of laughs would be differentially affected by altering their duration properties. We expected that sped-up laughs (simulating increased call frequency capability potentially differentiated across the two vocal production systems), would be judged as more likely to be spontaneous (experiment 2). Finally, we slowed down the same laugh stimuli significantly, making them more difficult to identify as human laughs, and asked participants whether the vocalizations were from a human or a nonhuman animal (experiment 3). Because spontaneous laughs are driven by evolutionarily older neural pathways that are shared with many other animals, we expected that slowed-down spontaneous laughs would be indistinguishable from nonhuman animal vocalizations and that volitional laughs would be recognizable as human vocalizations.

2. Laughter stimuli

Spontaneous and volitional laughs were taken from two different sources. A laugh bout is a series of calls (sometimes called bursts). Typically, a voiced bout has initial call features with set pitch and loudness values that decay over time, often with a declination on both physical dimensions. See Fig. 1 for a spectrogram of a spontaneous laugh with illustrations of relevant features described above.

2.1.1. Spontaneous laughs

Eighteen spontaneous laughs, all from different speakers, were selected from 13 conversations between female speakers who were friends at the time of the conversation, and received course credit for their participation. The conversations were digitally recorded to DAT (16-bit amplitude resolution, 44.1 kHz sampling rate, uncompressed wav files, Sony DTC series recorder) using lapel microphones (Sony ECM-77B) placed approximately 15 cm from the mouth. Recordings were made in a quiet room in the Fox Tree Laboratory at UC Santa Cruz in 2002. Conversationalists had been instructed to talk about bad roommate experiences, and/or any other topics they desired. For more details on the conversations, see Bryant (2010). Eighteen laughs were selected based on having at least 2 laugh calls and no more than 10, all calls being voiced, and no overlapping speech or laughter. All introductory breaths and recovery breaths at the end of laughs were included. In all cases, selected calls were clearly individuated from surrounding speech or other laughter. Of the laughs selected, the speakers were, at the time, friends for an average of 11.9 months, and their mean age was 18.4 years ($SD = 0.78$).

2.1.2. Volitional laughs

Eighteen volitional laughs were selected from a collection of prompted laugh recordings made in the context of another project on women's vocal attractiveness. In this experiment, undergraduate women (mean age \pm SD = 19.6 \pm 2.7) performed several tasks including being digitally recorded reading scripted sentences and monophthong vowels (M-Audio Microtrack recorder, 16-bit amplitude resolution, 44.1 kHz sampling rate, uncompressed wav files). Recordings were made in a quiet room in the Haselton Lab at UCLA using an AKG E535 condenser microphone placed approximately 15 cm from the mouth. After these recordings were made, women were instructed verbally by a female research assistant to "Now laugh" with no other prompting. Out of 64 total women who performed this task, 18 were selected for the current study. The selected laugh bouts were chosen based on having at least 2 calls and no more than 10, and all calls being voiced. As in the spontaneous laughs, all introductory breaths and recovery breaths were included. Age variance in the two groups (spontaneous versus volitional) was not equal (Levene's test: $F = 4.52$, $p = 0.02$), but the means were not significantly different (independent samples t-test: $t_{19.79} = 1.75$, $p = 0.09$).

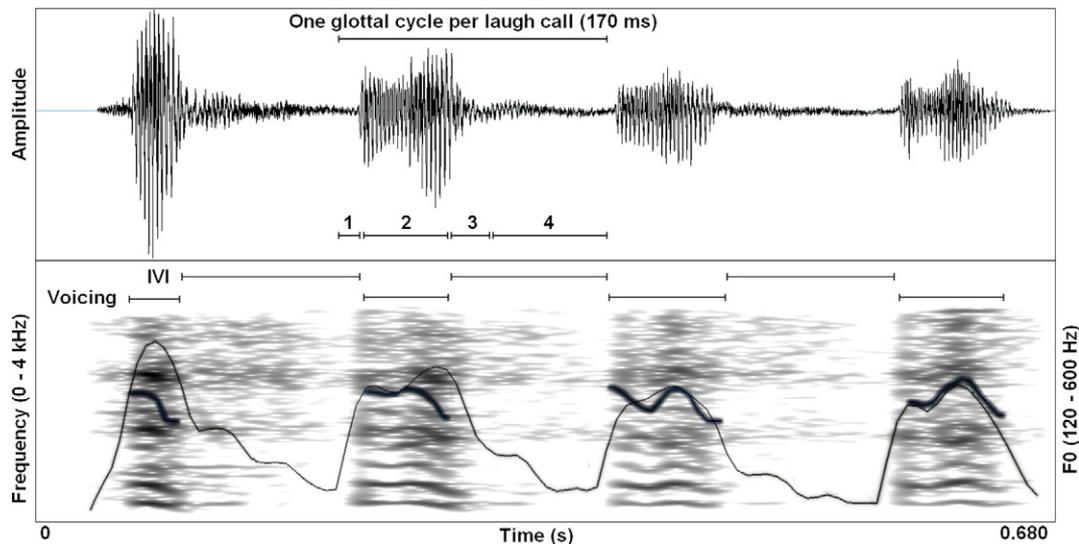


Fig. 1. Sample waveform and narrowband FFT spectrogram (30 ms Gaussian analysis window, 44.1 kHz sampling rate, 0–4 kHz frequency range) of 680 ms spontaneous laugh bout containing four calls. One glottal cycle (170 ms) represented with four stages: 1) adduction (closing) 2) voicing 3) abduction (opening) 4) pause. IVI: Intervoicing intervals. Broken lines over voiced segments represent fundamental frequency contours (F_0 : 120–600 Hz), and continuous line represents intensity contour (dB).

2.2. Acoustic analysis

Acoustic analyses were performed on all laughs using Praat, version 5.3.01 (Boersma & Weenink, 2011). See Table 1 for acoustic data.

2.2.1. Duration

Bout duration for each laugh was measured from the onset of visible acoustic energy as viewed in a spectrogram (FFT method, window length: 0.005 s., time steps: 1000, frequency steps: 250, Gaussian window shape, dynamic range: 50 dB) to the offset of energy in the final call, or bout-final inspiratory element. Calls were counted based on audible and visible separated voiced energy. Mean call duration was calculated as total bout duration divided by call number. Mean intervoicing interval (IVI) was calculated as the summed lengths of all unvoiced intervals between calls (i.e., voiced call offset to voice call onset) divided by call number minus one. Unvoiced portions were determined by a lack of formant structure as viewed through a spectrogram with settings described above, and lack of periodicity with standard pitch range values. Rate of intervoicing interval (rate of IVI) for each laugh bout was calculated using the following formula:

$$\frac{\left(\frac{\sum x_i}{(c-1)}\right)}{\left(\frac{d}{c}\right)}$$

where x_i are the intervoicing interval values, c is the total call number, and d is the bout duration of the series. This measure captures the averaged rate of unvoiced segments per call across a laugh bout.

2.2.2. Loudness and pitch

Loudness variability was measured as decibel (dB) standard deviation (SD), but overall loudness was not considered because laugh types were acquired using different recording apparatus that affects absolute recording levels. F_0 analysis was calculated across all voiced portions of the laugh bouts using the Praat autocorrelation algorithm with recommended pitch range values for adult women (120–600 Hz).

2.3. Statistical analyses

For statistical analysis, F_0 values were converted to semitones (relative to 50 Hz). All acoustic variables were normally distributed (Shapiro–Wilk test) except mean call duration, mean IVI, and rate of IVI which were log-transformed. To eliminate inter-correlations between our eleven acoustic measures, we used principal components

analysis (PCA) without rotation. The analysis generated four components with an eigenvalue greater than 1 (Kaiser's criterion), and these four factors accounted for 87% of the variance in the dataset. Variables were associated with a factor if they loaded with a value greater than 0.6. See Table 2 for PCA values. Factor 1 included mean F_0 , F_0 minimum, and F_0 maximum. Factor 2 included F_0 standard deviation (SD), F_0 range (F_0 max– F_0 min), mean IVI, and bout duration. Factor 3 included rate of IVI, and call number, and Factor 4 included only mean IVI.

ANOVA tests revealed that Factor 1 was significantly different between the laugh types (ANOVA: $F_{1,34} = 13.74, p < 0.005, \eta^2 = 0.29$) with all included F_0 values being higher in spontaneous laughs than volitional laughs. Factor 3 was also significantly different between laugh types (ANOVA: $F_{1,34} = 4.14, p < 0.05, \eta^2 = 0.13$) with call number and proportion IVI both higher in spontaneous laughs. Factors 2 and 4 were not significantly different across the two laugh types (Factor 2 ANOVA: $F_{1,34} = 2.44, p = ns, \eta^2 = 0.07$; Factor 4 ANOVA: $F_{1,34} = 0.46, p = ns, \eta^2 = 0.01$).

Post hoc tests were performed on the five individual variables that loaded on to the significant components (factors 1 and 3). The false discovery rate (q) adjustment was used for each of the five t-tests ($q = [p \times n]/i$) where p is original p -value, n is number of total comparisons, and i is the rank of each p -value (Benjamini & Hochberg, 1995). Significance was set at $q = .05$. Rate of IVI was higher in spontaneous laughs than volitional laughs (independent samples t-test: $t_{34} = 3.56, q = 0.005, d = 1.19$) as were F_0 mean (independent samples t-test: $t_{34} = 2.62, q = 0.033, d = 0.87$), and F_0 maximum (independent samples t-test: $t_{34} = 2.57, q = 0.025, d = 0.85$). F_0 minimum and call number were not significantly different across laugh types (both $t_s < 2$).

3. Experiment 1

We examined whether the set of spontaneous and volitional laughs described above could be perceptually distinguished.

3.1. Method

3.1.1. Participants

Sixty-three participants (20 male, 43 female; mean age = 18.6 years, range = 17–23) took part in the experiment and received credit in an introductory communication course at UCLA. Participants were recruited for a study called “Fake laughs.”

3.1.2. Procedure

The experiment was presented using SuperLab 4.0 (www.superlab.com) on an iMac desktop computer in an experimental cubicle in a quiet room. Participants wore headphones (Sony MDR-V250) and loudness levels were checked prior to each session. The 36 laughs (amplitude normalized) were presented in random order, and after each laugh, participants were asked to decide whether the laugh was “real” or “fake” by pressing either “1” for “real” or “0” for “fake” on a computer keyboard. After each rating, participants were asked to rate their confidence in their decision (these data are not reported in the results) and then prompted for the next trial to ensure they were ready.

Table 2

Orthogonal acoustic dimensions generated from principal components analysis.

Factor	Eigenvalue	Variance (%)	Acoustic features loading (> 0.6)
1*	3.22	29.26	F_0 mean, F_0 maximum, F_0 minimum
2	2.98	27.11	F_0 SD, F_0 range, mean IVI, bout duration
3*	1.91	17.38	Rate of IVI, call number
4	1.50	13.60	Mean IVI

Note: Factors that differed between laugh types denoted by * = $p < 0.01$.

Table 1

Acoustic analysis data for spontaneous and volitional laughs.

Acoustic Dimensions	Laugh Type	
	Spontaneous	Volitional
Pitch (Hz)		
F_0 Mean	343 (56.9)	295 (62.6)
F_0 SD	42.6 (15.8)	30.8 (15.0)
F_0 Minimum	268 (49.4)	239 (55.1)
F_0 Maximum	422 (74.4)	361 (76.9)
F_0 Range	154 (52.2)	122 (47.7)
Loudness		
dB SD	7.6 (1.6)	9.9 (1.4)
Duration		
Call number	4.2 (1.2)	3.6 (1.0)
Bout duration (ms)	891 (353.5)	907 (235.3)
Mean call duration (ms)	216 (66.1)	265 (77.7)
Mean intervoicing interval (IVI) (ms)	90.2 (50.4)	72.5 (22.3)
Mean rate of IVI per bout (%)	0.42 (0.16)	0.28 (0.07)

Note: All variances equal. Standard deviations in parentheses.

3.2. Results

Participants' overall accuracy for judgments of whether laughs were spontaneous (real) versus volitional (fake) ($M \pm SD = 67\% \pm 0.11$) were significantly better than chance (50%) (one-sample two-tailed t -test: $t_{125} = 17.6, P < 0.0001, d = 1.55$). Accuracy was significantly higher when the correct answer was "real" ($M \pm SD = 71\% \pm 0.10$) rather than "fake" ($M \pm SD = 63\% \pm 0.10$), and this difference was also significant ($t_{62} = 4.26, P < 0.0001, d = 0.80$). There was a slight bias to answer "real" in the task (54%) that could account for this difference however. To assess the bias, criterion (c) was calculated ($0.5[Z_H + Z_{FA}] - 1 = 2.3$) (Stanislaw & Todorov, 1999) indicating that just under half of the difference between accuracy rates for spontaneous versus volitional laughs was due to the bias.

The PCA analysis revealed that spontaneous laughs were higher in pitch with three F_0 variables loading onto factor 1, and this factor correlated positively with judgments of being "real" ($r = 0.56, P < 0.001$). In addition, laughs that had a higher rate of unvoiced segments per call (rate of IVI) were rated as more "real" ($r = 0.39, P < 0.05$). There were no sex differences in the judgments of the laughs.

4. Experiment 2

In experiment 2 we examined whether accelerated speed differentially affected judgments of spontaneity in laughter. We expected that if volitional laughter production was constrained by limited control over laryngeal musculature underlying glottal adduction cycling rate, then faster calls should be perceived as more spontaneous. We therefore predicted that participants would judge sped-up spontaneous laughs more accurately but be more likely to judge volitional laughs as "real," making those judgments less accurate.

4.1. Method

4.1.1. Participants

Seventy-seven participants (34 male, 43 female; mean age = 19.4 years, range = 18–29) took part in the study and received credit in an introductory communication course at UCLA.

4.1.2. Stimuli

The spontaneous and volitional laughs from experiment 1 were sped-up digitally with pitch held constant using the Adobe Audition 2.0 (www.adobe.com) constant stretch effect function (stretching mode: time stretch, high precision, splicing frequency: 51 Hz, overlapping: 30%). Duration was reduced 33% for all laughs, reflecting approximately 1.2 standard deviations in the mean call duration across all laughs in the experiment. The entire laugh sequence was altered at once so call duration and intercall intervals were changed equivalently. The duration alteration amount was used in order to achieve a salient perceptual difference across all laugh pairs, but retain laugh speeds that did not exceed the normal range of human laughter (Bachorowski et al., 2001). The manipulated versions retained the formant structure, fundamental frequency values, and rate of IVI of their original counterparts. In particular, rate of IVI remained the same because intercall intervals changed in linear proportion to bout length. Essentially, the laughs were changed acoustically *only* on the dimension of speed which resulted in shorter call and intercall durations, and the laughs sounding faster overall. See Fig. 2 for an example of one spontaneous laugh and one volitional laugh (sound files in supplementary materials, available on the journal's website at www.ehbonline.org) before and after the manipulations in experiments 2 and 3. Experiment 2 consisted of 18 laughs in each of the four conditions: spontaneous normal, spontaneous fast, volitional normal, and volitional fast. Laughs were divided into two counterbalanced lists so participants did not hear the same laugh twice (i.e., one normal

and one sped-up), resulting in each participant being exposed to only one version of each laugh.

4.1.3. Procedure

The experimental procedure was identical to experiment 1.

4.1.4. Results

Overall accuracy was similar to experiment 1 ($M \pm SD = 67\% \pm 0.16$). Fig. 3 shows the percentage of laughs judged as "real" across the four conditions. A repeated measures ANOVA was used with laugh type (spontaneous versus volitional), and speed (normal versus fast) as within-subject variables, subject sex as a between-subject variable, and percentage correct as the dependent measure. There was a main effect of laugh type (ANOVA: $F_{1, 75} = 11.22, P < 0.001, \eta^2 = 0.130$) with spontaneous laughs ($M \pm SD = 70\% \pm 0.15$) recognized at higher rates than volitional laughs ($M \pm SD = 63\% \pm 0.15$). Again, there was a slight overall bias to answer "real" (53%) ($c = 1.7$). There was also an effect of speed, with normal laughs ($M \pm SD = 69\% \pm 0.14$) being recognized at a higher rate than fast laughs ($M \pm SD = 64\% \pm 0.17$), (ANOVA: $F_{1, 75} = 8.96, P < 0.01, \eta^2 = 0.107$). As predicted, these variables interacted such that speed improved accuracy for spontaneous laughs, but decreased accuracy for volitional laughs (ANOVA: $F_{1, 75} = 27.16, P < 0.0001, \eta^2 = 0.266$) meaning that all laughs were judged as more "real" when they were sped-up. There were no sex differences in any of the conditions.

5. Experiment 3

Animals (including humans) can easily identify conspecific vocalizations, but through digital manipulation (e.g., temporal and frequency changes), altered vocalizations can retain many of their acoustic properties though cease to sound like the same species. Substantially altering vocal sounds can essentially prevent listeners from effortlessly identifying their origin, and force them to attend to specific acoustic properties more carefully. In experiment 3, we slowed down human laughs significantly, making them more difficult to identify as human vocalizations. Participants were then asked to identify these vocalizations as being either from a human or from a nonhuman animal. No previous research to our knowledge has examined judgments of whether stimuli were produced by human or nonhuman animals, but neuroimaging work has examined cerebral responses to nonhuman animal vocalizations relative to a variety of other stimuli including human voices (e.g., Lewis, Brefczynski, Phinney, Janik, & DeYoe, 2005; Altmann, Doehrmann, & Kaiser, 2007; Belin et al., 2008). De Lucia, Clarke, and Murray (2010) found that human and nonhuman animal vocalizations elicited early responses in statistically indistinguishable brain networks.

Differences in glottal and respiratory dynamics between spontaneous and volitional laughter likely contribute to perceptible differences between the laugh types. Consistent with this, we found that the averaged rate of unvoiced segments per call was higher in spontaneous laughter. Because spontaneous laugh production is thought to involve laryngeal neural pathways shared with nonhuman animal vocalizations, we expected that slowed-down spontaneous laughs would be relatively harder for participants to distinguish from nonhuman animal vocalizations. Conversely, we predicted that slowed-down volitional laughs would retain acoustic features associated with human speech (due to increased engagement of supralaryngeal articulators) and be judged as such.

5.1. Method

5.1.1. Participants

Seventy-three participants (14 males, 59 female; mean age = 19.2 years, range = 17–26) took part in an experiment called

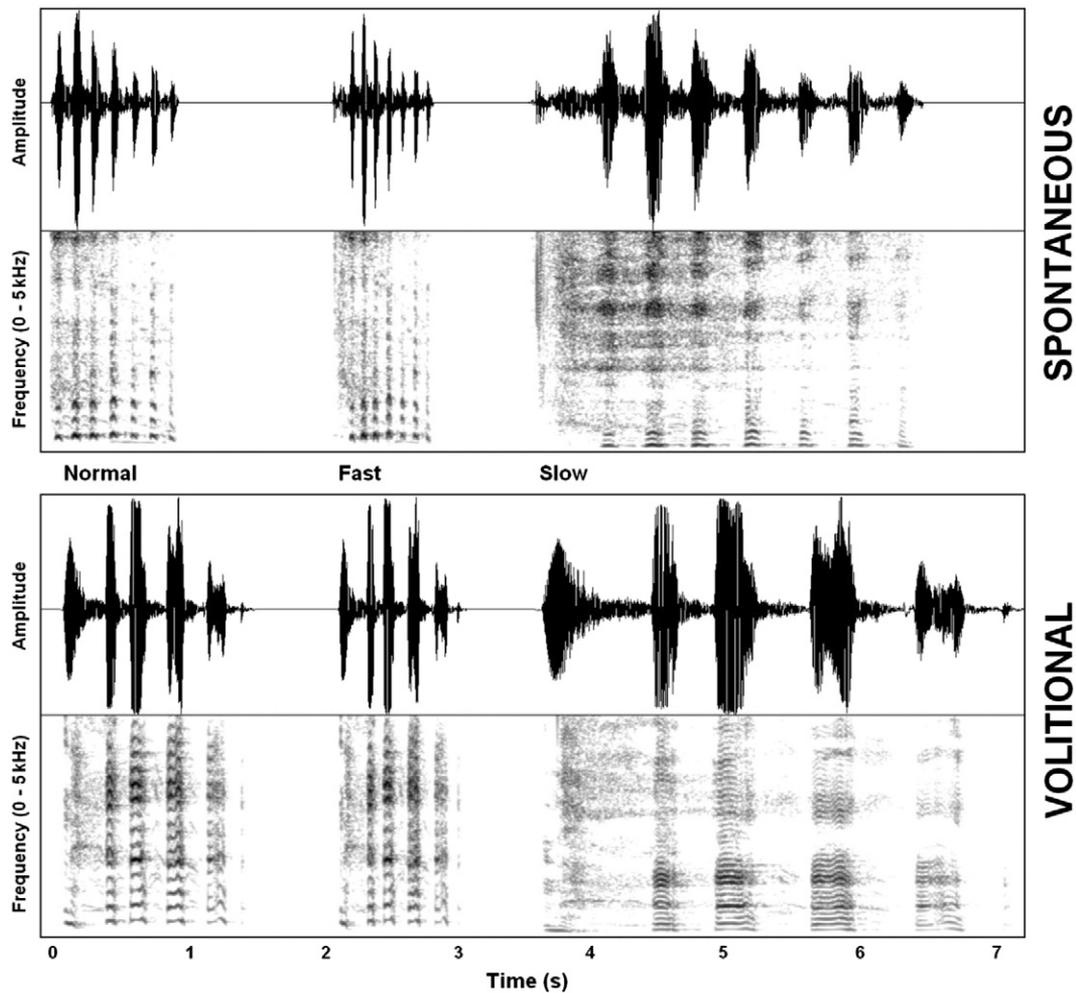


Fig. 2. Sample waveforms and narrowband FFT spectrograms (35 ms Gaussian analysis window, 44.1 kHz sampling rate, 0–5 kHz frequency range) of one spontaneous laugh, and one volitional laugh in normal (experiment 1), fast (experiment 2), and slow (experiment 3) conditions. Sound files of both laughs with manipulations available in supplementary materials.

“Human or animal?” and received credit in an introductory communication course at UCLA.

5.1.2. Stimuli

The spontaneous and volitional laughs from Experiment 1 were slowed down digitally using the Adobe Audition 2.0 constant stretch effect function (stretching mode: resample, high precision) with pitch changing in approximate linear proportion to length. Duration was increased 260% for all laughs which resulted in call and intercall durations increasing equivalently, but rate of IVI remained constant, again, because intercall intervals changed in linear proportion to bout length. The manipulations altered the vocalizations enough to make them not obviously produced by a human, but still within acoustic ranges found in other comparably-sized primate species (Hauser, 1993). Of particular importance, F_0 values were changed from a mean of 319 Hz to approximately 120 Hz mean overall.

5.1.3. Procedure

Testing context was identical to experiments 1 and 2. Once sitting at the computer, participants were instructed that they would hear digitally-altered recordings – some of humans, and some of nonhuman animals – and they were asked to make this distinction. Participants were presented with the 36 slowed laughs in random order. After each trial, they answered the question regarding whether the sound was from a human or nonhuman animal by pressing “0” for nonhuman animal and “1” for human on a computer keyboard. They

were then asked to rate their confidence in their decision. After the experiment they were asked to name any animals they believed they heard, and to identify what types of human vocalizations they believed they heard.

5.1.4. Results

Participants identified slowed spontaneous laughs as human at chance levels ($M \pm SD = 48\% \pm 0.18$), (one sample t-test: $t_{72} = 0.85, P = 0.39, d = 0.11$). But they identified slowed volitional laughs as human significantly greater than chance ($M \pm SD = 65\% \pm 0.18$), (one-sample t-test: $t_{72} = 6.88, P < 0.0001, d = 0.83$), and at a rate significantly higher than judgments of slowed spontaneous laughs (independent samples t-test: $t_{72} = 7.52, P < .0001, d = 0.94$). Fig. 4 shows the mean likelihood of judging laughs as being produced by a human or nonhuman animal across laugh types. Factor 1 from the PCA (pitch factor) was not correlated with judgments of the vocalizations being from a nonhuman animal ($r = 0.18, P = 0.31$) but the relative proportion of unvoiced segments per call (rate of IVI) did positively correlate with those judgments ($r = 0.34, P < 0.05$) (See Fig. 5 for a scatterplot of associations between rate of IVI and judgments from experiments 1 and 3). As in the first two experiments, there were no sex differences in participants’ judgments.

In the debriefing questionnaire, 47 participants identified one or more primate species, and another 19 identified non-primate animals (e.g., dogs, whales). Nine people reported that they believed all the recordings were of humans. Some reported that all the stimuli

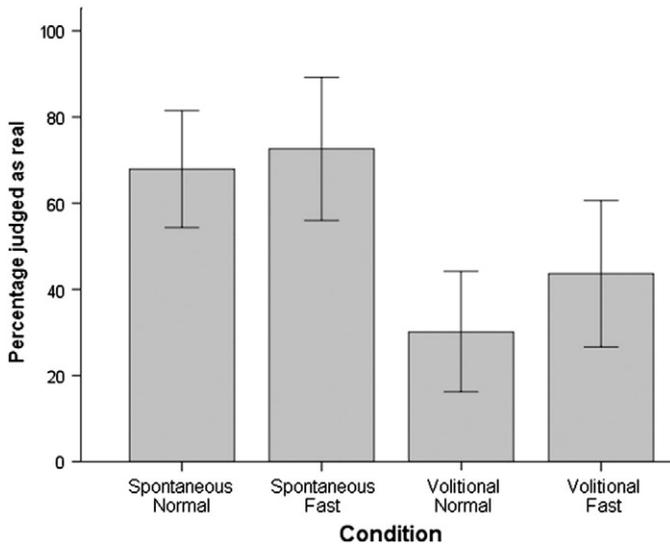


Fig. 3. Experiment 2 results showing percentage of laughs judged as “real” across four conditions. Ratings of “real” for volitional conditions calculated as $(1 - \text{hit rate})$. Error bars: ± 1 SD.

sounded quite similar and they had difficulty determining the source. When asked which human vocalizations they had heard in the experiment, 52 participants identified laughter, and 32 mentioned crying and/or yawning.

6. Discussion

Our findings demonstrate that people can accurately distinguish between spontaneous and volitional laughter, that sped-up laughs (both spontaneous and volitional) are rated as more “real,” and that listeners are more likely to mistake slowed-down spontaneous laughs (as opposed to volitional laughs) for nonhuman animal vocalizations. Spontaneous laughter had higher average pitch (F_0 mean) and higher maximum pitch (F_0 max) than volitional laughter, and also had a higher rate of intervoicing intervals per call (rate of IVI). Higher pitch in the spontaneous laughs used in our study might have reflected greater arousal in our recorded conversationalists relative to speakers asked to laugh on command. Pitch was also positively associated with judgments

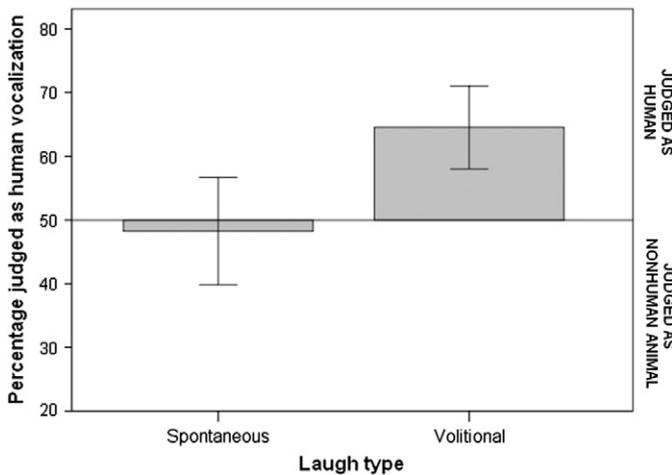


Fig. 4. Experiment 3 results showing percentage of slowed laughs judged as produced by a human (versus a nonhuman animal). 50% represents chance performance—above chance indicates judgment as human, and below chance indicates judgment as nonhuman animal. Error bars: ± 2 SE.

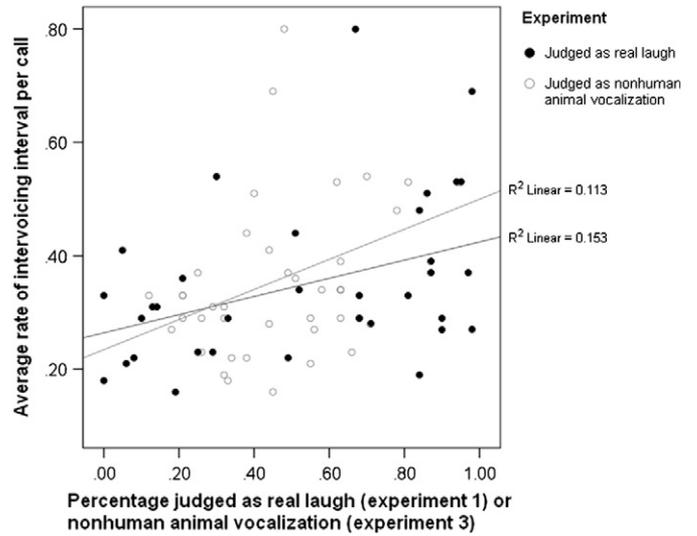


Fig. 5. Scatterplot of results from two experiments across laugh types. On the X-axis are data from Experiment 1 showing likelihood of judgments of laughs as “real” (versus fake) and Experiment 3 showing judgments of slowed laughs being produced by a nonhuman animal (versus human). On the Y-axis are data for each bout on average rate of intervoicing interval per call. This acoustic measure is related to judgments in both experiments.

of laughs being “real.” Arousal is likely a crucial component underlying the triggering of spontaneous laughter (Ruch & Ekman, 2001; Gervais & Wilson, 2005) so it might often be a reliable cue of speaker intentions. However, arousal might also be relatively easy to fake (Scherer, 2013), so there could be other important cues that perceivers use to discriminate between spontaneous and volitional laughter.

Spontaneous laughs had a higher average rate of unvoiced segments per call (rate of IVI) than volitional laughs and this measure correlated with judgments of being real (experiment 1) as well as judgments of being from a nonhuman animal (experiment 3). The importance of rate of IVI in these judgments could reflect the fact that unvoiced portions of the laughs contain sounds that reveal the dynamics of the mechanisms controlling respiratory and glottal activity. Spontaneous emotional vocalizations have different underlying neural and physiological control pathways than the speech system, so an adaptive perceptual design should be sensitive to those acoustic features that best distinguish spontaneous laughs from those produced volitionally. MacLarnon and Hewitt (1999) described the recent evolution of increased thoracic innervation in humans that serves fine breathing control during speech production. One consequence of slowed breathing for speech is the reduced presence of inspiratory elements between voiced speech segments. Nonhuman primate vocalizations, conversely, are typically shorter, and contain more inspiration between voiced units. Spontaneous laughter in humans likely reveals an effect of breath control relative to our closest primate cousins, which gives our laughs their human specific (i.e., ha ha) sound (Provine, 2000). Future work should address the question of whether there are specific acoustic attributes in the IVIs that are associated with these judgments. Additionally, rate of IVI might be an important feature that contributes to the contagiousness of laughter, constituting one important dimension in a putative “laugh detector” (Provine, 2000).

Behavioral and neuroanatomical evidence suggests that several reliably developing emotional vocalizations in humans, such as pain shrieks, crying, and spontaneous laughter are the products of a highly conserved vocal production system shared by most mammals (Fitch, 2006; Brudzynski, 2010; Owren, Amoss, & Rendall, 2011). But human speech ability evolved after our split from the common ancestor, and is implemented by direct neural connections between motor cortex

and laryngeal motor neurons—connections not shared with our closest primate relatives (Jurgens, 2002). The human speech system likely afforded the ability to reproduce many vocal calls, including laughter, formerly under the exclusive control of phylogenetically older connections between the periaqueductal gray (PAG) region and peripheral vocal anatomy. Thus, the differential control over breathing and supralaryngeal articulators likely results in perceptible acoustic distinctions in human speech that are not present in spontaneous emotional vocalizations.

Our data revealed that while participants can identify “real” and “fake” laughs better than chance, speakers are still quite adept at generating volitional laughs that sound real to listeners. Some level of deception is clearly occurring, with normal volitional laughs being judged as real on average 37% of the time suggesting the presence of a co-evolutionary arms race that likely shaped senders and receivers of a variety of volitionally controlled vocal signals, including cries, shrieks, sexual orgasm calls, and laughter. Theorists have previously proposed an arms race scenario for smiling (Owren & Bachorowski, 2001) and crying (Lummaa, Vuorisalo, Barr, & Lehtonen, 1998; Zeifman, 2001), among others. Though these vocal signals differ with regard to pitch, duration, and other dimensions, they might all have a spontaneous “instinctive” (Provine, 2012) version of the call as well as a volitionally produced version that mimics certain aspects of the phylogenetically older spontaneous call.

Spontaneous emotional signals evolve either by conveying reliable information to conspecifics who benefit from it (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005) or by inducing conspecifics to act in adaptive ways without actually transmitting discrete bits of information (Owren & Rendall, 2001). Reliability can be defined as a consistent relationship between a characteristic of a signal and the signaler or its environment, along with a benefit for receivers to detect this relationship (Searcy & Nowicki, 2005). But deceptive signaling (i.e., breaking the consistent signal-signaler relationship by design for individual benefit) can evolve depending on the relative costs and benefits of responses to signals resulting from different strategies. Because receivers do not typically have perfect information, and the costs of responses to deceptive signals can be relatively low, the benefits of responding to reliable signals can stabilize the signaling system while allowing for deception (Johnstone & Grafen, 1993).

In the case of humans, selection has likely acted on senders to deceptively produce fairly accurate volitional versions of emotional vocalizations through the speech system. This, in turn, puts selection pressure on receivers to resist being manipulated by these signals (Krebs & Dawkins, 1984), resulting in fine-tuned perception aimed at detecting dishonest signaling, as well as increasing acoustic resolution in producing believable facsimiles of their spontaneous counterparts (Tinbergen, 1952). The degree to which these signals can manifest with high acoustic accuracy is going to be a function of the ability of the speech system to copy the dynamics of emotional vocal control. There are many functional reasons that senders of laugh signals might want to produce them in contexts that do not ordinarily trigger their production. If spontaneous laughter originated from a highly conserved play signaling system shared by our closest primate relatives (e.g., the sound of labored breathing during physical play) (Provine, 2000), honest displays might function to guide adaptive behavior in receivers in the form of trust and cooperation. Several functions for human laughter have been proposed such as signaling playful and cooperative intent (Gervais & Wilson, 2005; Mehu & Dunbar, 2008), implicit preferences (Lynch, 2011), encrypted knowledge (Flamson & Barrett, 2008; Flamson & Bryant, 2013) or group coalitions (Bryant, 2012). Dishonest signals associated with communicative behaviors of affiliative intent could facilitate manipulative strategies, and we should expect vigilance that minimizes their effectiveness.

The current research represents the first demonstration that spontaneous laughter (i.e., laughter produced in natural contexts between familiar speakers) is perceptually distinguishable from

volitional laughter (i.e., laughter produced on command, inarguably deliberate and controlled). Moreover, we found that these laugh types were acoustically distinct, and differentially judged in a predictable way according to manipulations of duration properties. We also found that slowed down spontaneous laughs were perceptually indistinguishable from nonhuman animal vocalizations. Together these results suggest that spontaneous and volitional laughter are produced by different underlying neural control systems, with spontaneous laughter generated by phylogenetically older vocal production mechanisms. Future work should examine the differential neural underpinnings of these laugh types, including whether spontaneous laughs are under vagal rather than cortical control.

Our findings are based on judgments of female laughs by undergraduate participants. We limited this study to only female laughter for two reasons. First, we wanted to reduce extraneous acoustic variation between fake and real laughs, especially in the manipulations of experiment 3. Because pitch was also changed as a function of time, altered male laughs would have ended up far below typical mammalian F_0 values, which would have confounded perceptual judgments. Future work using the method can offset this problem by controlling pitch adjustment during speed manipulations in male laughter. Second, we wanted to reduce complications associated with cross sex communication dynamics. While we found no sex differences in judgments assessing women, research should examine possible crossover interactions between laugher and judges' sex. Additional research is also needed to determine whether our results generalize to judgments of laughter produced in other contexts. Important distinctions might be found across laughs produced in varying social contexts such as among friends, potential mates, coalition partners, and competitors. A more comprehensive analysis of a larger corpus of laughter (using both men's and women's laughs) will likely reveal systematic acoustic differences between these laugh conditions, and perhaps differences in perceivers' ability to distinguish between spontaneous and volitional laughs.

Additional laugh types should be examined as well, including quite notably, laughter induced by tickling that evokes distinctive cerebral responses (Szameitat et al., 2010). Volitional laughs likely also have specific communicative functions separate from mimicking spontaneous laughs, particularly in the context of speech in conversation. For example, “polite” laughs might often be prosocial signals despite not being spontaneous laughs. Laughter represents a complex suite of signals, some evolutionarily ancient and others relatively recent. A better understanding of laughter might provide important insights into the nature of human sociality and provide an invaluable piece in the puzzle of cooperative behavior.

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Appendix A

Sound files accompanying Fig. 2 available online: Real laugh sequence example.wav; Fake laugh sequence example.wav.

Appendix B

Data from all experiments and acoustic analysis available online.

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