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Report

Reconstructing the Evolution of Laughter in Great Apes and Humans

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Summary

Human emotional expressions, such as laughter, are argued to have their origins in ancestral nonhuman primate displays [1–6]. To test this hypothesis, the current work examined the acoustics of tickle-induced vocalizations from infant and juvenile orangutans, gorillas, chimpanzees, and bonobos, as well as tickle-induced laughter produced by human infants. Resulting acoustic data were then coded as character states and submitted to quantitative phylogenetic analysis. Acoustic outcomes revealed both important similarities and differences among the five species. Furthermore, phylogenetic trees reconstructed from the acoustic data matched the well-established trees based on comparative genetics. Taken together, the results provide strong evidence that tickling-induced laughter is homologous in great apes and humans and support the more general postulation of phylogenetic continuity from nonhuman displays to human emotional expressions. Findings also show that distinctively human laughter characteristics such as predominantly regular, stable voicing and consistently egressive airflow are nonetheless traceable to characteristics of shared ancestors with great apes.

Results

Acoustic Approach

The current work examined the acoustics of tickle-induced vocalizations from 21 infant and juvenile orangutans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), and bonobos (*P. paniscus*), as well as tickle-induced laughter produced by three human infants (see Figure 1 for representative spectrograms and Table S1 available online for subject and recording information). Tickle-induced vocalizations were also recorded from an individual lesser ape, a siamang (*Symphalangus syndactylus*).

Figure 2 compares the acoustics of these vocalizations across humans and apes on each of the 11 acoustic measures of this study (defined in Table S2; see Figure 1). As might be expected, the siamang values were closer to those of the orangutans than to any other species. Humans produced significantly more voiced sounds (with regular vocal-fold vibration) than any other species (Figure 2A). All three human participants exhibited predominantly such segments, whereas vocal-fold vibration patterns were overwhelmingly irregular and noisy among the great apes, with only one ape (a bonobo) emitting voiced sounds. Examining spectral-temporal patterning revealed that all species could emit calls with two or more vibration regimes (patterns of energy distribution over time) (Figure 2F). Humans produced more vibration regimes per call than did the apes, but the number of regimes were too low to be compared statistically. Statistical comparisons on other spectral variables showed no species-specific differences. Significant differences in temporal variables occurred only among the great apes. In comparison to orangutans, chimpanzees and bonobos exhibited shorter calls and intercall intervals (Figures 2G and 2H). Chimpanzees and bonobos also showed more calls per series than either gorillas or orangutans (Figure 2I). All species could emit two or more bouts per series (Figure 2J). Airflow results showed that all great apes produced both consecutive egressive calls (during exhalation phases) as well as alternating egressive-ingressive sounds (during exhalation-inhalation phases), with the latter being predominant in chimpanzees (Figure 2K). In contrast, humans emitted exclusively egressive laughter.

All great apes showed at least one instance of consecutive egressive tickle-induced calls lasting longer than 3 s. One gorilla and one bonobo even emitted consecutive egressive calls for stretches of more than 10 s (13.2 and 10.5, respectively), with expiration proportion of at least 0.66 and 0.80, respectively. The longest egressive call sequences of orangutans and chimpanzees lasted 4.2 s and 3.3 s, respectively.

Phylogenetic Approach

Phylogenetic trees reconstructed from the acoustic data are shown in Figure 3 and Figure S1. Exhaustive search with orangutans as the outgroup resulted in a single maximum-parsimony phylogram that placed humans closest to bonobos and chimpanzees and more distant from gorillas (treelength = 110; RI = 0.686; Figure S1A). With the siamang as the outgroup the data produced essentially the same single tree, but with orangutans falling furthest from humans (treelength = 113; RI = 0.750; Figure 3A). The similarity of these two phylograms lends credence to the overall approach and indicates that the more-inclusive reconstruction (siamang as outgroup; Figure 3) was most informative (see Experimental Procedures for information on outgroup selection). By additionally reconstructing cladograms with the bootstrap method, high bootstrap values (79%–97%) were obtained (see Figure 3B and Figure S1B), indicating well-resolved topologies and strong support for the internal clades [7, 8]. Characters providing the strongest data fit to the phylogenetic trees with consistent directional changes along the clades (i.e., highest RI values) were vibration regimes per call, call duration, and calls per series (see Table S3). The reconstructed trees were robust and replicated the tree topology produced previously by genetic relationships among great apes and humans (e.g., [9, 10]).

Discussion

Taken together, the acoustic and phylogenetic results provide clear evidence of a common evolutionary origin for tickling-induced laughter in humans and tickling-induced vocalizations

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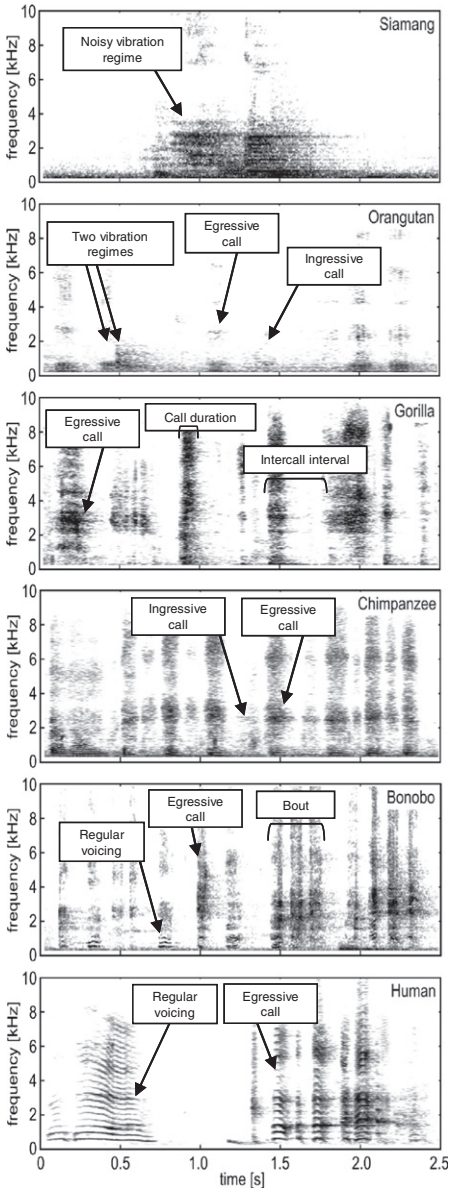

Figure 1. Representative Spectrograms of Great Ape, Human, and Siamang Vocalizations Elicited by Tickling

Recordings of these narrowband spectrograms (40 ms Hanning window) had a 22,050 Hz sampling rate. Great ape vocalizations include those of an orangutan, gorilla, chimpanzee, and bonobo.

in great apes. Although most pronounced acoustic differences were found between humans and great apes, interspecific differences in vocal acoustics nonetheless supported a quantitatively derived phylogenetic tree that coincides with the well-established, genetically based relationship among these species. At a minimum, one can conclude that it is appropriate to consider "laughter" to be a cross-species phenomenon, and that it is therefore not anthropomorphic to use this term for tickling-induced vocalizations produced by the great apes. This term has been used in previous work on tickle- and play-related vocalizations in several nonhuman species (e.g., [11–13]), and the current results provide clear support for such usage, at least as far as primates are concerned.

However, the results arguably compel much more substantive conclusions as well. For example, the acoustic variables found to most strongly distinguish humans and apes statistically (i.e., regular voicing and airflow direction) were not the characters showing the most consistent, directional change throughout the phylogenetic tree (i.e., vibration regimes per call, call duration, calls per series). In other words, the acoustic data supported at least two independent classifications—one based on general differences among all species, and one based on more extreme deviations occurring specifically in humans. A related point is that the two variables that did most clearly differentiate humans and apes also varied among the latter, but to a lesser degree. Thus, although orangutans and gorillas showed virtually no evidence of regular voicing, one of the bonobos did show this phenomenon. Regularity of vocal-fold vibration has also been found in previous work on chimpanzee laughter [14]. The data further indicate that an evidently ancestral condition included a mix of both egressive-ingressive and more consistently egressive laugh sounds, the former giving rise to characteristically alternating airflow in chimpanzee laughter and the latter to more purely egressive laughter in humans. These outcomes are inconsistent with Provine's [13] supposition that obligate alternating airflow represents the ancestral condition and is associated with an inherent neuromuscular constraint on ape vocalizations created by quadrupedalism.

We conclude that although tickling-induced human laughter, which is deeply grounded in human biology (e.g., [15]), is acoustically and perceptually distinct from homologous great ape sounds [13], the evolutionary changes occurred along existing dimensions of variation, rather than being de novo inventions. This inference is potentially significant for language evolution as well, because human speech is also marked by consistently regular vocal-fold vibration [16] and sustained, consistently egressive airflow [17, 18]. Although both aspects have been argued to be uniquely human traits [13, 16, 17], it appears unlikely that such is the case. Regular voicing has now been documented in a large number of nonhuman primate calls (e.g., [19–21]). The present study found that gorillas and bonobos were able to sustain egressive airflow 3–4 times longer than the total likely duration of the normal breath cycle, which for comparison is approximately 3.1 s in human children [22], while showing expiration proportions longer than the value of 0.61 reported for human children [22]. It is of course always difficult to determine whether changes such as the characteristic voicing and egressive airflow of human laughter represent adaptations or secondary outcomes of selection pressure on other traits, for example related to speech or other vocalizations. Nonetheless, the evidence unequivocally suggests a distinctive exaggeration of preexisting traits at some point after the divergence of hominins from a common ancestor with chimpanzees and bonobos, approximately 4.6 to 6.2 million years ago [23, 24].

Parenthetically, we should note that factors such as the lower larynx position of humans relative to great apes [25], body-size differences among the various species, and simple, within-species maturational effects do not readily account for the current results or associated theoretical interpretations. The most important differences noted here, for instance related to temporal organization and airflow, are unlikely to be importantly affected by changes in laryngeal position or body size. Vocal-fold response characteristics that bias their vibration toward more regular or noisier regimes could be so affected, but developmental observations suggest that this

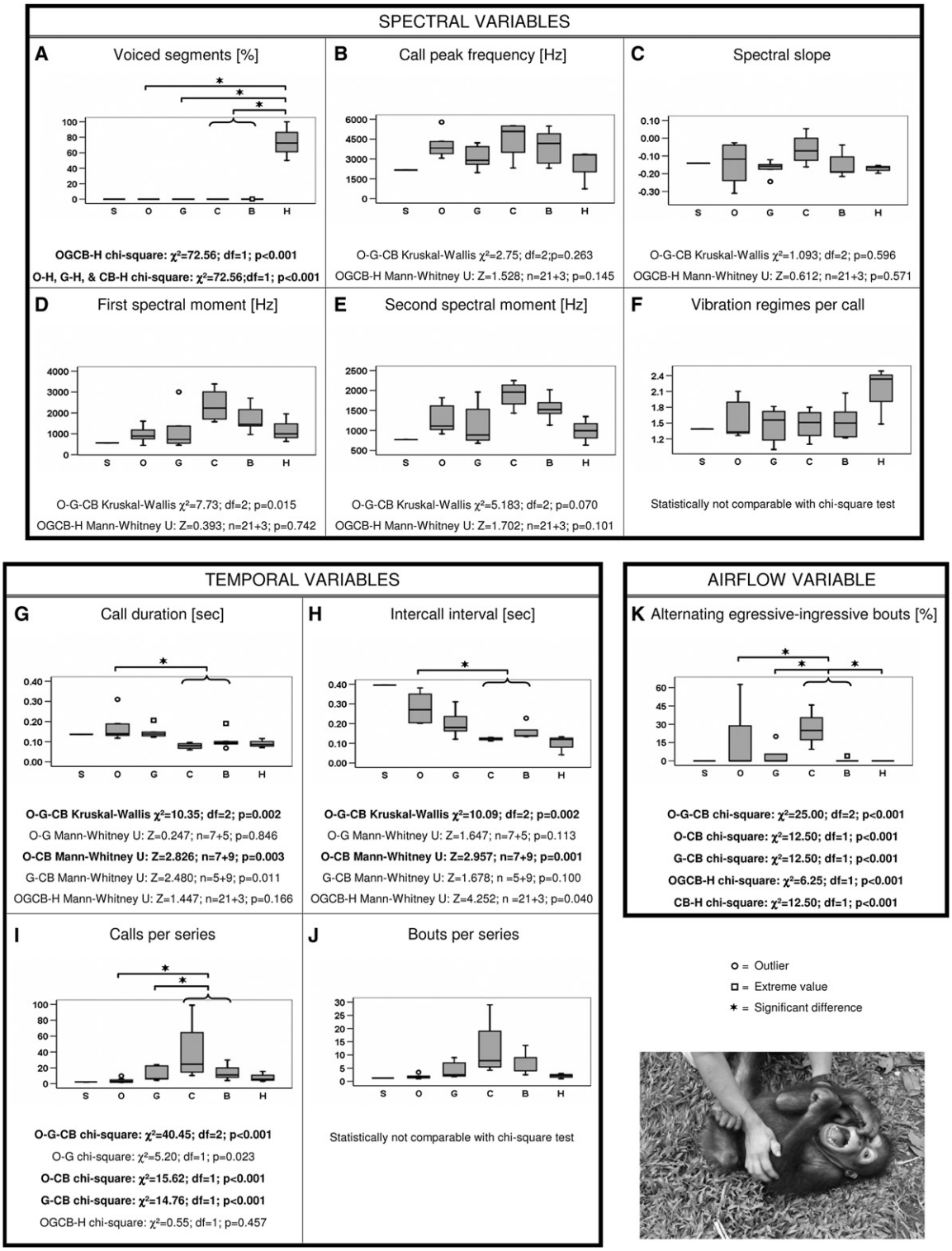

Figure 2. Species-Specific Comparisons for Each Measured Variable of Tickling-Elicited Sounds in Apes and Humans

Acoustic data of the respective spectral (A–F), temporal (G–J), and airflow (K) variables were statistically compared both among great apes (O, orangutan; G, gorilla; C, chimpanzee; B, bonobo) and between great apes and humans (H). Significant differences found with Hommel-Hochberg corrections are shown in bold font. Data of the siamang (S) were not assessed statistically, because only one individual had been included.

factor is also not important. Specifically, young humans like the ones recorded here appear much more likely than adults to display noisy vibration regimes that include ingressive sound production, as in high-arousal crying of typically developing infants [26, 27]. In other words, the consistently regular voicing that distinguished human laughter in the current study

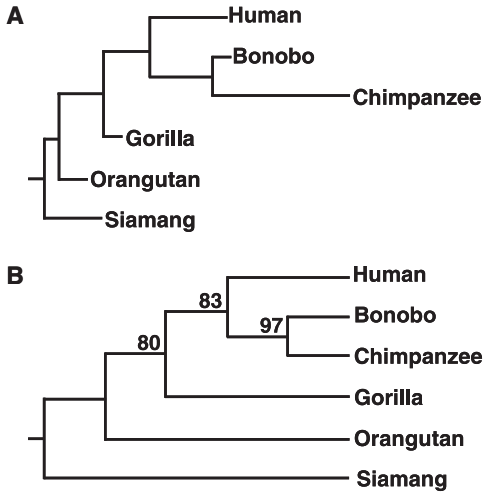

Figure 3. Reconstructed Trees of Apes and Humans with the Siamang as the Outgroup Derived with Tickling-Induced Vocalizations

(A) The single maximum-parsimony phylogram as a result of exhaustive search (treelength = 113, RI = 0.750). Shorter branches indicate fewer character state changes.

(B) Bootstrap cladogram as a consensus tree of 10,000 replicates. Bootstrap values for ingroup clades are shown just above their preceding branches.

occurs routinely across the life-span, independent of significant changes in body size, vocal-fold size, and evident vocal-fold response characteristics.

Summarizing, the results suggest that the evolutionary origins of human laughter can be traced back at least 10 to 16 million years [24, 28] to the last common ancestor of humans and modern great apes (see Figure 4 for a model of laughter evolution). However, the origins may be even earlier, because the tickling-induced vocalizations from the individual siamang showed many similarities to orangutan laughter. Given the general trends uncovered, the primordial laughter sounds of this common ancestor were likely to be generally longer and slower than those of humans and extant great apes, included a smaller number of more uniformly noisy calls with fewer changes in vibration regimes, and showed both alternating and more consistently egressive airflow. Consistent with the postulate of gradual evolutionary change from nonhuman displays to human emotional expressions by Darwin [3] and others [1, 2, 4–6], analyses indicated both that there is significant acoustic variation in the tickle-induced laughter of great apes and that distinctive features of human laughter could have been shaped through selection and exaggeration of preexisting traits. The question left unaddressed is of course why those particular acoustic properties emerged, and what functions they may have served as laughter became a pervasive and characteristic component of human social communication.

Experimental Procedures

Data Collection

Subjects were 22 infant and juvenile apes and 3 human infants (Table S1). The apes included 7 orangutans, 5 gorillas, 4 chimpanzees, 5 bonobos, and 1 siamang. All individuals were audio-recorded in their home facilities (or homes) while being tickled by familiar and mostly different humans, who were instructed to trigger tickle-induced vocalizations in the subjects as part of a playful social interaction, a method that has been effectively applied in a range of species [11–14] (see Figure 1 for representative spectrograms). Subjects were primarily tickled on their palms, their feet, their necks, or in their armpits. Table S1 includes further information about subjects and recordings.

Acoustic Analysis

Acoustic analysis was conducted with ESPS/waves+ ("xwaves") 5.3 software (Entropic Research Laboratory, Washington, DC). Calls were originally sampled at either 22,050 or 44,100 Hz and were standardized at the lower rate after conversion to ESPS format. Before analysis, all waveforms were subject to high-pass, 60 Hz filtering (removing any AC contamination) and centered around the zero-volt line (removing any DC offset). The amplitude of each file was then scaled relative to the full, 16-bit range. Finally, to ensure good recording quality in the final sample, the mean RMS amplitude of each call was compared to an adjacent, representative sample of background noise within the same file, and any sound for which this signal-to-noise ratio was less than 2 dB was excluded. The final sample included 829 calls.

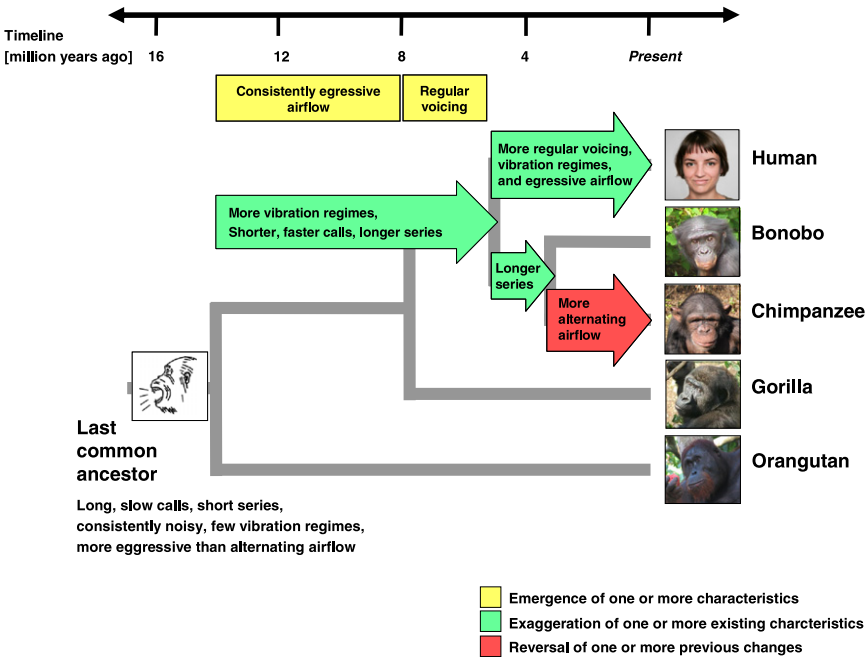

Figure 4. Model of Laughter Evolution Based on Both Acoustic and Phylogenetic Results of Tickling-Induced Vocalizations by the Hominidae

The phylogenetic emergence and modifications of laugh characteristics were reconstructed dating back to the last common ancestor of humans and extant great apes, around 10 to 16 million years ago [24, 28].

The acoustic measurements used were ones that could be applied to each of the species, and that were deemed most likely to capture similarities and differences among the sounds based on earlier work [13, 14, 29] and on preliminary examination of all species' vocalizations. Resulting measures were designed to particularly capture three dimensions of potential interest, including degrees of regularity of vocal-fold vibration, temporal organization of sounds, and airflow direction. Calls, bouts, and bout series were characterized with a set of 11 acoustic variables (defined in Table S2), including six spectrally related measures applicable for both voiced and unvoiced sounds (percent voiced segments, call peak frequency, spectral slope, first spectral moment, second spectral moment, and number of vibration regimes per call), four temporally related measures (call duration, intercall interval, calls per series, and bouts per series), and one categorical airflow variable (percent bouts with alternating egressive-ingressive calls). A call was defined as a temporally continuous acoustic element with endpoints defined by an energy increase at the start and decrease at the finish. A bout was defined as consecutive calls with spectral-temporal energy patterns that were either the same or showing gradual changes consistent with the vocal-folds not bifurcating to a qualitatively different vibration regime [30, 31]. A bout series then consisted of consecutive bouts spaced at intervals of less than 1 s. Measurements were made with displays that could as needed combine waveforms, narrowband spectrograms (40 ms Hanning window), spectral slices extracted from those spectrograms, and wideband spectrograms (8 ms Hanning window). Spectral slices and spectrograms were computed with full preemphasis.

One researcher first performed all measurements, and a second then independently repeated the particular measures in which human judgement might affect the outcome (voiced segments, vibration regimes per call, calls per series, bouts per series, and alternating egressive-ingressive bouts). Interobserver reliability was gauged with Cohen's kappa, and resulting values are in Table S2. For each measure, medians (if $n \leq 5$) or means (if $n > 5$) were first calculated by subject across all calls of each bout, then all bouts of each bout series, followed by calculating only medians across all bout series. Outcomes for ape subjects were compared both across species and to humans with chi-square (nominal data) and Kruskal-Wallis (ordinal data) tests. Post-hoc comparisons for the two data types were conducted with chi-square and Mann-Whitney U tests, respectively. Hommel-Hochberg corrections were applied to adjust α levels as needed for repeated comparisons. Finally, to capture any evidence of potential flexibility in airflow direction, instances of continuously egressive call sequences within a series were tallied for each individual. The longest duration of each egressive call sequence (from start of first call to end of last call) was then calculated for each species, as well as the expiration proportion associated with this sequence (the cumulative duration of egressive calls divided by the duration of the sequence).

Phylogenetic Analyses

Phylogenetic analyses were performed to reconstruct possible evolutionary trees based on the acoustic data of the study species with PAUP* 4.0 software (Sinauer Associates, Sunderland, MA). Although vocal behavior is often analyzed as part of understanding primate phylogenetic relationships (e.g., [20, 32]), our approach was critically different, namely the use of the already well-established phylogeny of humans and great apes as a reference in interpreting any phylogenetic relationships potentially found among their ticking-induced vocalizations. In these analyses, measured variables (i.e., characters) were first coded as character state values, followed by reconstructing the possible phylogenetic trees.

Acoustic values were averaged by subject in form of means and then standardized with log(x+1) transformations [33]. Based on these transformed values, species medians were calculated for each variable and coded as character states ranging from 0 to 9 (a total of 10 states) via Thiele's [33] gap-weighting method. The gap-weighting method weighs gaps between coded states of species by giving larger weights to larger differences in trait values [33]. Trait values of largest difference, i.e., the smallest and highest values of a trait, were first coded as character states 0 and 9, combined indicating the largest gap. The remaining values of the trait were then coded as states between 0 and 9, with dependence on the distances to the smallest and highest trait values.

Trees were then reconstructed and rooted with a preselected, outgroup species. Exhaustive search was applied to obtain the best data fit of all possible trees (e.g., [34]) by using the maximum-parsimony method to find the tree of fewest character state changes, meaning shortest treelength (e.g., [35]). Bootstrap analysis was then performed to test the robustness [7] of each candidate clade (an ancestor and its descendants) by reconstructing an additional tree as a consensus of 10,000 newly generated replicates. For each replicate, one randomly selected character was deleted while one randomly selected character was added [7]. Confidence (bootstrap) values represented the proportion of clades recovered in all replicates [7]. In this analysis, the bootstrap value associated with a given clade is the percentage of replicate trees in which it appears, and only clades with bootstrap values equalling or exceeding 50% were retained (50% majority rule). Clades with bootstrap values of 70% or higher are defined as well-supported [8].

The character fit to the most parsimonious tree(s) was measured by the retention index (RI) [36], which reflects the number of collectively derived character states [37]. The RI index is defined as $(g - s)/(g - m)$, where s is the number of steps a character requires in a specific tree, g is the maximum number of steps a character requires in any tree, and m is the minimum number of steps a character requires in any tree [37]. An RI value of 1 indicates the absence of homoplasy, which occurs when character states evolve more than once. As the amount of homoplasy increases, associated RI values approach 0. High RI values are thus indicative of consistent, directional character state changes along the clades and strong data fit to the tree(s). Characters without RI values are parsimony uninformative and show a maximum of one ingroup species with a character state different from the other ingroup species. It is therefore possible for parsimony-uninformative characters to become parsimony-informative when adding taxonomic units to the data set.

Analyses were conducted twice, first with the seven orangutan subjects as the outgroup and gorillas, chimpanzees, bonobos, and humans as the ingroup, and then with the single siamang subject as the outgroup, with orangutans, gorillas, chimpanzees, bonobos, and humans making up the ingroup. The rationale was that finding the same topology in each case would increase confidence in the reliability of the phylogenetic results, particularly if adding orangutans to the ingroup and with the siamang as the outgroup in the second analysis confirmed and extended the first, less-inclusive reconstruction.

Supplemental Data

Supplemental Data include one figure and three tables and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01129-4.

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References

1. Andrew, R.J. (1963). The origin and evolution of the calls and facial expressions of the primates. Behaviour *20*, 1–107.
2. Chevalier-Skolnikoff, S. (1973). Facial expression of emotion of nonhuman primates. In Darwin and Facial Expression: A Century of Research in Review, P. Ekman, ed. (New York: Academic Press), pp. 11–89.
3. Darwin, C. (1872). The Expression of Emotion in Man and Animals (London: Murray).
4. Gervais, M., and Wilson, D.S. (2005). The evolution and functions of laughter and humor: A synthetic approach. Q. Rev. Biol. *80*, 395–430.

5. Redican, W.K. (1975). Facial expressions in nonhuman primates. In Primate Behavior: Developments in Field and Laboratory Research 4, L. Rosenblum, ed. (New York: Academic Press), pp. 103–194.
6. van Hooff, J.A.R.A.M. (1962). Facial expressions in higher primates. Symp. Zool. Soc. Lond. *8*, 67–125.
7. Felsenstein, J. (1985). Confidence limits on phylogenies: A method using the bootstrap. Evolution Int. J. Org. Evolution *39*, 783–791.
8. Hillis, D.M., and Bull, J.J. (1993). An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst. Biol. *42*, 182–192.
9. McBrearty, S., and Jablonski, N.G. (2005). First fossil chimpanzee. Nature *437*, 105–108.
10. Wildman, D.E., Uddin, M., Liu, G., Grossman, L.I., and Goodman, M. (2002). Implications of natural selection in shaping 99.4% nonsynonymous DNA identity between humans and chimpanzees: Enlarging genus Homo. Proc. Natl. Acad. Sci. USA *100*, 7181–7188.
11. Panksepp, J. (2007). Neuroevolutionary sources of laughter and social joy: Modeling primal human laughter in laboratory rats. Behav. Brain Res. *182*, 231–244.
12. Preuschoft, S., and van Hooff, J.A.R.A.M. (1995). Homologizing primate facial displays: A critical review of methods. Folia Primatol. (Basel) *65*, 121–137.
13. Provine, R.R. (2000). Laughter: A Scientific Investigation (New York: Viking Press).
14. Vettin, J., and Todt, D. (2005). Human laughter, social play, and play vocalizations of non-human primates: An evolutionary approach. Behaviour *142*, 217–240.
15. Provine, R.R., and Emmorey, K. (2006). Laughter among deaf signers. J. Deaf Stud. Deaf Educ. *11*, 403–409.
16. Lieberman, P. (1975). On the Origins of Language: An Introduction to the Evolution of Human Speech (New York: Macmillan).
17. MacLarnon, A., and Hewitt, G.P. (1999). The evolution of human speech: The role of enhanced breathing control. Am. J. Phys. Anthropol. *109*, 341–363.
18. Winkworth, A.L., Davis, P.J., and Adams, R.D. (1995). Breathing patterns during spontaneous speech. J. Speech Hear. Res. *38*, 124–144.
19. Braune, P., Schmidt, S., and Zimmermann, E. (2008). Acoustic divergence in the communication of cryptic species of nocturnal primates (*Microcebus* ssp.). BMC Biol. *6*, 19.
20. Davila Ross, M., and Geissmann, T. (2007). Call diversity of wild male orangutans: A phylogenetic approach. Am. J. Primatol. *69*, 305–324.
21. Owren, M.J., Seyfarth, R.M., and Cheney, D.L. (1997). The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cynocephalus ursinus*): Implications for production processes and functions. J. Acoust. Soc. Am. *101*, 2951–2963.
22. Fokkema, D.S., Maarsingh, E.J.W., van Eykern, L.A., and van Aalderen, W.M.C. (2006). Different breathing patterns in healthy and asthmatic children: Responses to an arithmetic task. Respir. Med. *100*, 148–156.
23. Chen, F.C., and Li, W.H. (2001). Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. Am. J. Hum. Genet. *68*, 444–456.
24. Stauffer, R.L., Walker, A., Ryder, O.A., Lyons-Weiler, M., and Blair Hedges, S. (2001). Human and ape molecular clocks and constraints on paleontological hypotheses. J. Hered. *92*, 469–474.
25. Fitch, W.T. (2000). The evolution of speech: A comparative review. Trends Cogn. Neurosci. *4*, 258–267.
26. Grau, S.M., Robb, M.P., and Cacace, A.T. (1995). Acoustic correlates of inspiratory phonation in infant cry. J. Speech Hear. Res. *38*, 373–381.
27. Robb, M.P. (2003). Bifurcations and chaos in the cries of full-term and pre-term infants. Folia Phoniatr. Logop. *55*, 233–240.
28. Goodman, M., Porter, C.A., Czelusniak, J., Page, S.L., Schneider, H., Shoshani, J., Gunnell, G., and Groves, C.P. (1998). Towards a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. Mol. Phylogenet. Evol. *9*, 585–598.
29. Bachorowski, J.-A., Smoski, M.J., and Owren, M.J. (2001). The acoustic features of human laughter. J. Acoust. Soc. Am. *110*, 1581–1597.
30. Fitch, W.T., Neubauer, J., and Herzel, H. (2002). Calls out of chaos: The adaptive significance of nonlinear phenomena in mammalian vocal production. Anim. Behav. *63*, 407–418.
31. Wilden, I., Herzel, H., Peters, G., and Tembrock, G. (1998). Subharmonics, biphonation, and deterministic chaos in mammal vocalization. Bioacoustics *9*, 171–196.
32. Zimmermann, E. (1990). Differentiation of vocalizations in bushbabies (Galaginae, Prosimiae, Primates) and the significance for assessing phylogenetic relationships. Z. Zool. Syst. Evolutionsforsch. *28*, 217–239.
33. Thiele, K. (1993). The holy grail of the perfect character: The cladistic treatment of morphometric data. Cladistics *9*, 275–304.
34. Saitou, N., and Imanishi, T. (1989). Relative efficiencies of the Fitch-Margoliash, maximum-parsimony, maximum-likelihood, minimum-evolution, and neighbor-joining methods of phylogenetic tree construction in obtaining the correct tree. Mol. Biol. Evol. *6*, 514–525.
35. Maddison, D.R., and Maddison, W.P. (2000). MacClade 4: Analysis of Phylogeny and Character Evolution (Sunderland: Sinauer Associates).
36. Nei, M., and Kumar, S. (2000). Molecular Evolution and Phylogenetics (New York: Oxford University Press).
37. Farris, J.S. (1989). The retention index and the rescaled consistency index. Cladistics *5*, 417–419.