The evolution of laughter in great apes and humans

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It has long been claimed that human emotional expressions, such as laughter, have evolved from nonhuman displays. The aim of the current study was to test this prediction by conducting acoustic and phylogenetic analyses based on the acoustics of tickle-induced vocalizations of orangutans, gorillas, chimpanzees, bonobos and humans. Results revealed both important similarities and differences among the various species’ vocalizations, with the phylogenetic tree reconstructed based on these acoustic data matching the well-established genetic relationships of great apes and humans. These outcomes provide evidence of a common phylogenetic origin of tickle-induced vocalizations in these taxa, which can therefore be termed “laughter” across all five species. Results are consistent with the claims of phylogenetic continuity of emotional expressions. Together with observations made on the use of laughter in great apes and humans, findings of this study further indicate that there were two main periods of selection-driven evolutionary change in laughter within the Hominidae, to a smaller degree, among the great apes and, most distinctively, after the separation of hominins from the last common ancestor with chimpanzees and bonobos.

Researchers have long noted that emotional expressions in humans and displays in nonhuman primates can be similar in both form and context,1 leading many to suggest common phylogenetic origins.2-5 Human smiling and laughter have received much of the attention,6-8 with the case for homologies strengthened by evidence of strong cross-species similarities in the production anatomy of both facial9,10 and vocal11 expressions. The current work focused on laughter in particular, testing the hypothesis of phylogenetic continuity as directly as possible by measuring the acoustics of tickling-induced vocalizations in humans and all four great ape species, and then submitting the results to quantitative phylogenetic analyses.12

Laughter was deemed a strong candidate for phylogenetic reconstruction, as these sounds are deeply grounded in human biology.13,14 Vocalizations referred to as “laughter” also occur in great apes engaged in tickling and social play.5,7,15 Vettin and Todt16 have shown key similarities in the respective acoustics of play- and tickling-induced vocalizations in juvenile chimpanzees (Pan troglodytes) and tickling-induced laughter in adult humans.

The current work investigated tickling-induced laughter and vocalizations in humans and apes, based on collecting and analyzing these sounds from all four great ape species for the first time. The goal was to situate the origin and evolution of laughter within the larger phylogeny of the Hominidae by using obtained acoustic data as raw material, first for cross-species acoustic comparisons and then for quantitative phylogenetic reconstructions. The phylogenetic analyses of this study notably differed from earlier approaches. While vocal data previously helped to reconstruct the phylogeny of species and populations,17-19 the present study used the already well-established phylogeny of humans and great apes as a reference to measure the evolutionary relationship of vocal expressions. In all, 21 infant and juvenile orangutans (Pongo pygmaeus), gorillas (Gorilla gorilla), chimpanzees and

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Orangutans and gorillas also showed fewer calls per vocalization series and more egressive calls than chimpanzees and bonobos. Phylogenetic analyses based on the acoustic data replicated the already well-established genetic relationships among the five species, placing humans closest to bonobos and chimpanzees, more distant from gorillas, and furthest from orangutans (two exhaustive searches with the maximum-parsimony method, treelength = 110–113, retention index = 0.686–0.750). The resulting trees indicated well-resolved topologies and strong support for the associated clades (bootstrap value of 79–97%). Acoustic characters found to be most important to phylogenetic trees with the most consistent directional changes (highest retention index values) were the number of vibration regimes per call, call duration and the number of calls per series.

Taken together, the acoustic and phylogenetic results of this study provide evidence of common ancestry for laughter in humans and tickling-induced vocalizations in great apes and, consequently, support the more general claim of phylogenetic continuity from nonhuman displays to human emotional expressions.1-5 “Laughter” therefore is not an anthropomorphic term, and can instead arguably be traced as a vocalization type back to at least the last common ancestor of modern great apes and humans, approximately ten to sixteen million years ago.21,22

The data of the present study further suggest that the distinctive characteristics of human laughter, such as voicing and airflow direction, emerged from preexisting acoustic traits. While speech-related selection could have been a driving force for these changes,23 it should also be noted that there are key differences in the occurrence of laughter between humans and great apes. Whereas apes laugh primarily in the contexts of social play and tickling, laughter of humans occurs across a wide range of contexts.24,25 This dramatic expansion of laughter production most likely occurred in an intermediate hominin species, suggesting that selection could have been acting directly on these sounds. Notably, human infants also produce whoops, pleasure cries and hics when tickled,26 vocalizations that seem to be absent in the apes.

**Figure 1.** Representative spectrograms (40-ms Hanning window) of tickle-induced vocalizations from four great ape species and humans. Recordings had a 22,050-Hz sampling rate. This illustration first appeared as Figure 1 in Davila Ross et al.20
A close relationship between acoustic and context-related differences in laughter also seems to be present between the Asian and African great apes. In addition to producing the most distinctive laughter among the great apes, orangutans clearly were the species to laugh least during the tickling sessions, instead they predominantly produced squeaks. This behavioural pattern seems to extend to social play as well. 

In other words, all tickle-induced vocalizations occurring among non-human primates cannot be considered homologous to human laugh sounds. By extension, the evolutionary relation between primate laughter and tickle-induced calls produced by other species such as flying foxes (Pteropus conspicillatus, see video supplement) and rats should also be specifically tested using acoustically based phylogenetic analyses before conclusions are drawn concerning potential homologies.

This seemingly strong link between the form and function of laughter across great apes and humans suggests that the phylogenetic changes of laugh acoustics implicated in the current work were primarily a product of adaptation. We suggest that there were likely two main kinds of change in laughter acoustics and behaviour over the past ten to sixteen million years while other tickle- and play-induced vocalizations evolved. It remains unknown whether laughter and squeaks emerged prior to or in the common ancestor of great apes and humans. Notably, lesser apes produce tickle-induced vocalizations that acoustically resemble orangutan laughter (e.g., Symphalangus syndactylus; Davila Ross et al.; Hylobates lar; Zimmermann pers. obs.) and squeak-like calls during play (Nomascus spp.; Thomas Geissmann, pers. comm.). The figure is adapted from Davila Ross et al. Figure 4.

Figure 2. Model of the evolution of laughter and other vocalizations of tickling and play in great apes and humans. Two main periods of acoustic and function-related changes in laughter were likely to have occurred within the past ten to sixteen million years while other tickle- and play-induced vocalizations evolved. It remains unknown whether laughter and squeaks emerged prior to or in the common ancestor of great apes and humans. Notably, lesser apes produce tickle-induced vocalizations that acoustically resemble orangutan laughter (e.g., Symphalangus syndactylus; Davila Ross et al.; Hylobates lar; Zimmermann pers. obs.) and squeak-like calls during play (Nomascus spp.; Thomas Geissmann, pers. comm.). The figure is adapted from Davila Ross et al. Figure 4.

Supplementary materials can be found at: www.landesbioscience.com/supplement/RossCIB3-2-Sup.wmv

Note

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