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Higher fundamental frequency in bonobos is explained by larynx morphology

Sven Grawunder[1,8,9], Catherine Crockford[1,10,*], Zanna Clay[2], Ammie K. Kalan[1], Jeroen M.G. Stevens[3,4], Alexander Stoessel[5,6,7], and Gottfried Hohmann[1,11,*]

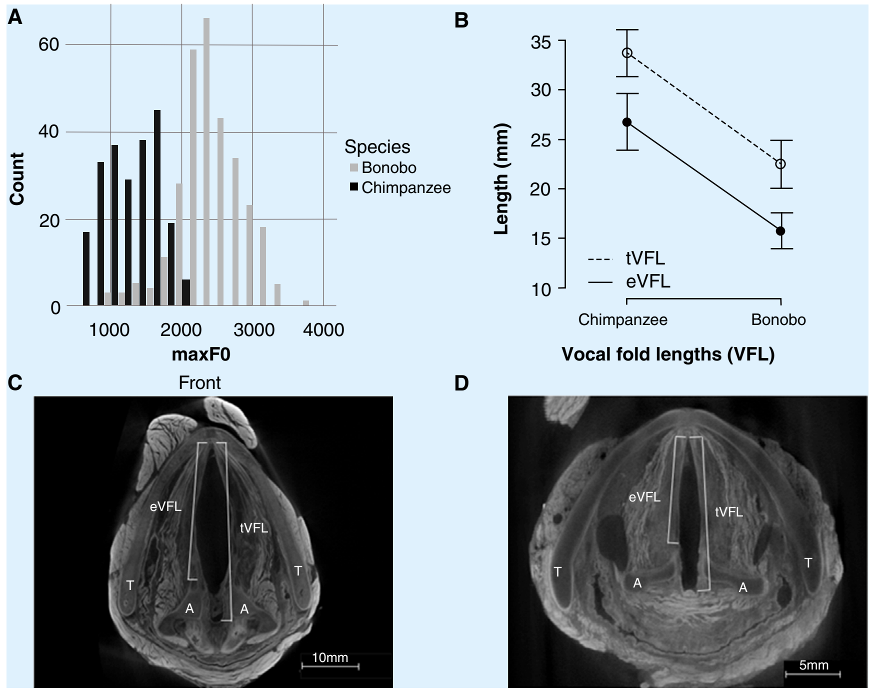

Figure 1. Comparison of chimpanzee and bonobo vocalizations and vocal folds.
(A) Distribution of maximum fundamental frequency values for chimpanzees and bonobos. (B) Measures of vocal fold length (VFL) per species: mean of total VFL (tVFL) and effective (anterior membranous) VFL (eVFL) with error bars showing a 95% confidence interval. (C,D) Vocal folds shown in a transverse CT scan for (C) female chimpanzee KAI and (D) female bonobo JAS. Labels indicate the arytenoid cartilages (A) and the thyroid cartilage (T).

Acoustic signals, shaped by natural and sexual selection, reveal ecological and social selection pressures [1]. Examining acoustic signals together with morphology can be particularly revealing. But this approach has rarely been applied to primates, where clues to the evolutionary trajectory of human communication may be found. Across vertebrate species, there is a close relationship between body size and acoustic parameters, such as formant dispersion and fundamental frequency (f0). Deviations from this acoustic allometry usually produce calls with a lower f0 than expected for a given body size, often due to morphological adaptations in the larynx or vocal tract [2]. An unusual example of an obvious mismatch between fundamental frequency and body size is found in the two closest living relatives of humans, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). Although these two ape species overlap in body size [3], bonobo calls have a strikingly higher f0 than corresponding calls from chimpanzees [4]. Here, we compare acoustic structures of calls from bonobos and chimpanzees in relation to their larynx morphology. We found that shorter vocal fold length in bonobos compared to chimpanzees accounted for species differences in f0, showing a rare case of positive selection for signal diminution in both bonobo sexes.

To assess the extent of between-species differences in f0, we analyzed loud calls with the highest and lowest f0 for each species (high hoots and low hoots of bonobos, pant hoots and roars of chimpanzees) recorded from wild populations of both species (Supplemental Information; Data S1). Using linear mixed models to test for species and sex differences in the maximum f0 of calls, we found that bonobo vocalizations were close to one octave higher than corresponding chimpanzee calls (full vs null model results: $\chi 2 = 176.73$, df = 3, $p < 0.0000$; Figure 1; Supplemental Information; Data S1). In addition, sex differences were evident in the maximum f0 in chimpanzee but not bonobo calls, with chimpanzee males having a higher f0 than females (Supplemental Information; Data S1).

Across species, a strong determinant of f0 is vocal fold length [5,6]. We measured the total vocal fold length (tVFL) and effective vocal fold length (the anterior membranous portion of the vocal fold that oscillates during vocalization; eVFL) of larynxes from bonobos (*n* = 7) and chimpanzees (*n* = 7), obtained from zoo facilities (Figure 1; Data S1), and compared them using unpaired two-tailed t tests, adjusted using Bonferroni correction. We derived morphometric measures from post mortem μCT scans of extracted larynxes (*n* = 12), or from full body scans (*n* = 2) acquired with a medical CT device. In bonobos, total vocal fold length as well as effective vocal fold length were significantly shorter than those of chimpanzees (Figure 1, Data S1; tVFL bonobo 22.5 mm ± 2.65 mm *versus* tVFL chimpanzee 33.7 ± 2.54, t(12) = 8.12, df = 11, p < 0.001; eVFL bonobo 15.7 mm ± 2.00 mm *versus* eVFL L 26.8 mm ± 2.67 mm, t(11) = 8.50, df = 11, $p < 0.001$). Yet, eVFL:tVFL ratios were similar in both species ($p = 0.083$) which implies there are no significant shape differences in vocal fold anatomy. The f0 of a call is largely defined by the eVFL, the shorter the eVFL found in bonobos corresponds well with the higher f0, and both measures deviate markedly from the corresponding values of chimpanzees. The relationship between f0 and vocal fold length of other African apes is similar to that of the chimpanzees in our study [5]. This suggests that the high f0 and the short vocal fold length of bonobos are derived traits.

Our results do not support several hypotheses that might account for species differences in f0. First, differences are unlikely a result of selection for efficient sound propagation in forest habitats where transmission of low f0 calls is more efficient than calls with a high f0 [7]. Whilst chimpanzees and bonobos both live in dense forest habitats, chimpanzees are also found in more open habitat. However, comparisons of chimpanzee populations living in these different habitats do not show dramatic differences in maximum f0 [8]. Second, it has been proposed that loud calls with a high f0 may signal physical strength and endurance in males [6]. While strength may explain sex differences in loud calls of chimpanzees [9], where male calls reach a higher f0 than female calls (Supplemental Information; Data S1), the f0 in corresponding bonobo calls is similar for males and females (Supplemental Information; Data S1), suggesting that in bonobos signaling physical strength is not a sexually-selected trait.

The high f0 vocalizations and shorter larynxes in bonobos show partial consistency with the self-domestication hypothesis, which implies the retention of juvenile traits in adults and has recently been suggested for bonobos [10]. However, in bonobos, high f0 is equally prominent in females and males, suggesting selection for high f0 has occurred in both sexes. Predictions of the self-domestication hypothesis may thus actually apply to both sexes. While acoustic body size exaggeration is well documented in various taxa of vertebrates, including primates [5], the results of our study are novel in representing a case of positive selection for signaling diminution.

Our results show that high f0 calls in both male and female bonobos correspond to short vocal fold length and cannot be fully explained by acoustic hypotheses of environmental influence, sexual selection nor the self-domestication hypothesis. Future studies will need to determine what females and male bonobos gain from signalling with a high f0. One possibility is that high f0 determines physical strength and endurance in both sexes and that this gives individuals an advantage when communicating within or between groups, and may facilitate co-dominance between males and females. If this was the case, achieving higher f0 through strength implies the use of greater lung capacity rather than vocal fold length reduction. We argue that reducing vocal fold length to achieve higher f0 more likely mimics juvenile vocal quality. We suggest an alternative explanation. Bonobos of both sexes are noticeably more tolerant and less violent to conspecifics than chimpanzees, both within and between groups. Thus, the high f0 may signal social tolerance or appeasement within and between groups.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures, one figure and one table can be found with this article online at https://doi.org/10.1016/j.cub.2018.09.030.

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[1]Department of Primatology, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany. [2]Durham University, Department of Psychology, UK. [3]Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, Belgium. [4]Behavioral Ecology and Ecophysiology Group, University of Antwerp, Wilrijk, Belgium. [5]Department of Human Evolution, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany. [6]Institute of Zoology and Evolutionary Research, Friedrich Schiller University, Jena, Germany. [7]Department of Archaeogenetics, Max-Planck-Institute for the Science of Human History, Jena, Germany. [8]Department of Human Behavior, Ecology and Culture, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany. [9]Department of Linguistics, Kiel University, Kiel, Germany. [10]Tai Chimpanzee Project, Centre Suisse de Recherches Scientifiques, Cote d'Ivoire.
[11]Lead Contact.
*E-mail: crockford@eva.mpg.de (C.C.), hohmann@eva.mpg.de (G.H.)