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**Chimpanzee lip-smacks confirm primate continuity for
speech-rhythm evolution**

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Ethics

Does your article include research that required ethical approval or permits?:

Yes

Statement (if applicable):

Permission to collect video data had been previously obtained from the authors' institutions (either for other projects or routine data collection) and all the relevant bodies responsible for managing research at each population. All procedures followed the Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research (Animal Behaviour, 2018, 135, I-X), all institutional guidelines, the legal requirements of the countries in which the work was carried out, and was granted ethical approval by the Biology Animal Welfare Ethical Review Board (AWERB), University of York.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:

Yes

Statement (if applicable):

All data needed to evaluate the conclusions in the paper are present in the paper and in the Supplementary Materials.

Conflict of interest

I/We declare we have no competing interests

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The authors declare that they have no conflict of interest.

Authors' contributions

This paper has multiple authors and our individual contributions were as below

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ASP and EK conducted analyses and wrote the paper. CH and KES provided materials and wrote the paper. ARL conceived the study, conducted analyses and wrote the paper.

1 Chimpanzee lip-smacks confirm primate continuity for speech- 2 rhythm evolution

3

4 André S. Pereira^{1,2}, Eithne Kavanagh³, Catherine Hobaiter¹, Katie E. Slocombe³, Adriano R.
5 Lameira^{1,4*}

6

7 ^{1.} School of Psychology and Neuroscience, University of St Andrews, St Andrews, United
8 Kingdom.

9 ^{2.} School of Biological Sciences, University of Aberdeen, Aberdeen, United Kingdom

10 ^{3.} Department of Psychology, University of York, York, United Kingdom

11 ^{4.} Department of Psychology, University of Warwick, Coventry, United Kingdom

12

13 *Corresponding author: adriano.lameira@warwick.ac.uk

14

15

16 Abstract

17

18 Speech is a human hallmark, but its evolutionary origins continue to defy scientific explanation.
19 Recently, the open-close mouth rhythm of 2-7 Hz (cycles/second) characteristic of all spoken
20 languages has been identified in the orofacial signals of several nonhuman primate genera,
21 including orangutans, but evidence from any of the African apes remained missing.
22 Evolutionary continuity for the emergence of speech is, thus, still inconclusive. To address this
23 empirical gap, we investigated the rhythm of chimpanzee lip-smacks across four populations
24 (two captive and two wild). We found that lip-smacks exhibit a speech-like rhythm at ~4 Hz,
25 closing a gap in the evidence for the evolution of speech-rhythm within primate order. We
26 observed sizeable rhythmic variation within and between chimpanzee populations, with
27 differences of over 2Hz at each level. This variation did not result, however, in systematic
28 group differences within our sample. To further explore the phylogenetic and evolutionary
29 perspective on this variability, inter-individual and inter-population analyses will be necessary
30 across primate species producing mouth signals at speech-like rhythm. Our findings support
31 the hypothesis that speech recruited ancient primate rhythmic signals and suggest that multi-
32 site studies may still reveal new windows of understanding about these signals' use and
33 production along the evolutionary timeline of speech.

34 Introduction

35

36 Throughout history, few traces for the evolution of speech have been found among nonhuman
37 primates (hereafter primates), obscuring the precursors and processes through which our
38 species came to develop a unique and powerful signal system. The last few decades have,
39 however, seen promising new advances (1–4). A research frontier that has gradually yielded
40 some of the most compelling evidence is the study of the evolutionary origin of speech-rhythm,
41 i.e., the fast open-close mouth cycles characteristic to each and every spoken language in the
42 world (5). This rhythm is inherent to speech and universal across spoken languages because it
43 expresses the production of syllables, where the opening and closing of the mouth roughly
44 correspond to vowel and consonant production, respectively (6, 7). This rhythm typically
45 exhibits a rate of 2-7 Hz, i.e., 2 to 7 open-close mouth cycles per second (5), and is a visual and
46 acoustic signal of speech that appears to be critical to its intelligibility (8–10).

47 Speech-like rhythm has been uncovered in a growing number of primate signals: lip-
48 smacks of various macaque species (11, 12), stump-tailed macaques' panting calls (12),
49 gelada's wobbles (13), gibbon song (14) and orangutan clicks and faux-speech (15). Further
50 studies have shown that, in macaques, lip-smacks develop along a similar trajectory to human
51 speech (16) and activate an area homologous to Broca's (17), with individuals being
52 perceptually attuned to lip-smacks' natural frequency (18). Together, these convergent lines of
53 evidence across fields and taxa indicate, on the basis of homology, that speech-rhythm likely
54 derived from ancient fast-paced mouth signals from deep within the primate lineage (19–21).
55 The overall validity of this hypothesis for the evolution of speech-rhythm and the assumption
56 of evolutionary continuity across fast-paced mouth movements in primates rest, however, on a
57 last phylogenetic steppingstone for which there is currently no data: the African great apes, the
58 closest extant hominid lineage to humans.

59 Here, to directly explore this gap in knowledge, we characterize the rhythm of
60 chimpanzee (*Pan troglodytes* spp) lip-smacks – affiliative signals typically produced by
61 groomers during social grooming (22, 23).

62

63 Methods

64 *Study subjects and data collection*

65 We identified lip-smack bouts present in video recordings collected at Edinburgh Zoo (*Pan*
66 *troglodytes verus* and one hybrid, UK) (Table 1) during August and September 2013 with a

67 Panasonic HDC SDX1; at Leipzig Zoo (*P. t. verus*, Germany) (Table 1) during June and July
 68 2017 with a Panasonic HDC-SD90 camcorder with a Sennheiser MKE 400 microphone
 69 attached; and in the wild in the Kanyawara community (*P. t. schweinfurthii*, Kibale National
 70 Park, Uganda) (Table 1) during December 2014 and August and September 2016 with a
 71 Panasonic HDC-SD90 camcorder with a Sennheiser MKE 400 microphone attached; and from
 72 the Waibira community (*P. t. schweinfurthii*, Budongo Forest Research, Uganda) (Table 1)
 73 community during December 2011, March 2012, December 2014, and August 2017 with a
 74 Panasonic SD90. All videos were 25 frames per second. Videos were selected for analysis
 75 when the face of the emitter was clearly visible during lip-smack production and this was the
 76 sole criteria to include a bout in the analysis. There was no proactive selection of particular
 77 individuals. All videos had been collected during opportunistic observation of the subjects'
 78 behaviour.

79 Permission to collect video data had been previously obtained from the authors'
 80 institutions (either for other projects or routine data collection) and all the relevant bodies
 81 responsible for managing research at each population. All procedures followed the Association
 82 for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals
 83 in Research (Animal Behaviour, 2018, 135, I-X), all institutional guidelines, the legal
 84 requirements of the countries in which the work was carried out, and was granted ethical
 85 approval by the Biology Animal Welfare Ethical Review Board (AWERB), University of
 86 York.

87

88 Table 1. *Lip-smack data used for analysis.*

Population	# individuals	# bouts (# open-close mouth cycles)/individual
<i>Edinburgh</i>	3 (1 female, 2 males)	<i>Female</i> : 8(49) <i>Males</i> : 16(104), 7(53.5)
<i>Leipzig</i>	3 (1 female, 2 males)	<i>Female</i> : 6(24) <i>Males</i> : 1(3), 1(9)
<i>Kanyawara</i>	5 (1 female, 4 males)	<i>Female</i> : 1(5) <i>Males</i> : 2(6), 2(8), 1(5), 1(3)
<i>Waibira</i>	3 (1 female, 2 males)	<i>Female</i> : 1(2) <i>Males</i> : 2(9), 5(25)

89

90

91 *Data analyses*

92 We used Filmora9 (Wondershare Technology Co., Shenzhen) to extract all identified lip-smack
93 bouts from the grooming bout videos. We used the *VideoReader* function to load all lip-smack
94 videos to MATLAB R2018a (MathWorks, Natick, MA) and extracted all frames of each bout.

95 To investigate whether chimpanzee lip-smacks exhibit a speech-like rhythm, we
96 calculated the dominant frequency of lip-smacking behaviour by extracting the power spectral
97 density, i.e., the quantity of power for each frequency component of a signal, of all lip-smack
98 bouts and then calculating its peak, which reflects the most representative frequency of mouth
99 aperture, and which we considered to be the approximate rate of mouth oscillation across lip-
100 smack bouts (15, 16). To do this, we used the *imtool* function to load all frames individually to
101 MATLAB and used the *Measure Distance* tool to measure the distance between a fixed point
102 in the top lip and a fixed point in the bottom lip of the emitter (15, 16, 18) (S2 Supplementary
103 Material, Fig. S1). For open-mouth cycles in which lip movement did not match jaw
104 displacement, we measured the distance between a point in the lower lip and the most fixed
105 and easily identifiable point of the video (e.g., the nasion or the glabella), which allowed us to
106 capture the movements of opening and closing of the jaw (16, 18). For the frames in which the
107 marking points were not clearly visible, we estimated mouth displacement to be the mean of
108 the adjacent frames (15). This estimation was possible because there was never more than one
109 consecutive frame during which we couldn't identify the marking points.

110 For each bout, we used the mouth displacement measurements to construct a time-series
111 of mouth displacement (15, 16, 18) (S1 Supplementary Material). To allow for comparability
112 between bouts, we normalized the amplitude of every time-series so that the mouth
113 displacement measures of each time-series varied between 0 and 100. We did so by subtracting
114 the minimum mouth displacement measurement of each time-series from all its mouth
115 displacement measurements and followed by setting all measurements as a percentage of the
116 maximum mouth displacement measurement of the series (16). For each time-series, we
117 subtracted the mean of all normalized mouth displacement measurements from each
118 normalized measurement to eliminate the D-C offset (i.e. mean amplitude displacement from
119 zero) and, thus, avoiding getting 0 as the dominant frequency. Subsequently, we used
120 MATLAB's *fft* function to perform a fast Fourier transform (FFT) of each time-series (16) (S2
121 Supplementary Material). We set the "NFFT", a parameter that defines the frequency scale of
122 the *fft*, to 1024 for every time-series, a value large enough to allow good resolution of the signal
123 in all series without compromising computational time. We squared the magnitude of each
124 time-series' FFT to obtain the series' power spectrum density (S2 Supplementary Material).

125 Finally, we used the R package *ggplot2* (24) to plot the smoothed out mean \pm 95%
126 confidence interval of the standardized power spectrum density of all time-series and used
127 custom R scripts to find the peak of the curve, i.e., the dominant frequency of chimpanzee lip-
128 smacking behaviour. We standardized all power spectrum density curves by standardizing the
129 spectral power variation (Y-axis) from 0 to 100 following the procedure previously described
130 for the standardization of the time-series. This standardization allowed us to account for the
131 relative spectral power at all frequencies of all bouts while avoiding having individual curves
132 contributing differently to the mean curve. To help visualize the data, we used the same
133 procedure to plot the mean \pm 95% confidence interval of the power spectrum density of all
134 time-series of each individual in each population, as well as of each pair of populations. All
135 time-series and each time-series' plot and power spectrum density plot can be found in S1
136 Supplementary Material. All code and steps to replicate the analysis described here are
137 available in S2 Supplementary Material.

138 To statistically compare frequency peaks between captivity and the wild, we used the
139 *glmer* function from the R package *lme4* (25) to build a generalized linear mixed model, which
140 we set up with a gamma error structure and inverse link function; the peak of each individual
141 bout was input as the dependent variable; population (Edinburgh, Leipzig, Kanyawara or
142 Waibira) was input as a fixed factor, and the identity of each individual was input as a random
143 factor to control for repeated measures. We confirmed that the distribution of the residuals was
144 normally distributed and that there was no issue of overdispersion. The code for this analysis
145 can be found in S2 Supplementary Material. Because the highest peak of some individual lip-
146 smack bouts reflected the distribution of inter-bout intervals (typically <1Hz) instead of the
147 real peak, which is a regular occurrence in studies of speech rhythmicity (e.g. 14), we assessed
148 all bouts individually and, for such deviant cases, only included the peaks of the dominant
149 frequency plot (S1 Supplementary Material) that corresponded to the true mean of open-mouth
150 cycles per second, as observed from each bout's time-series (S1 Supplementary Material).

151

152

153 Results

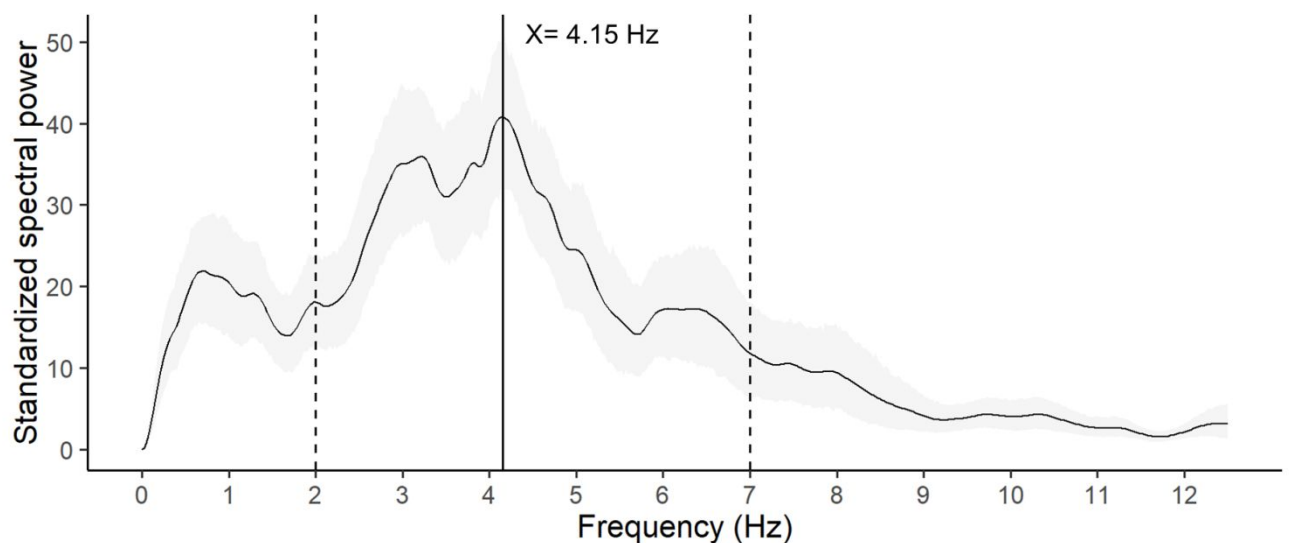
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155 We found that chimpanzee lip-smacks exhibited a mean rhythm per bout of 4.15Hz (Fig. 1).

156 We identified rhythm variation in lip-smack rate production across individuals who exhibited

157 the behaviour within and across populations (Fig. 2). For each of the populations, individual
158 lip-smack rhythm spanned a frequency range of at least 1Hz, with maximum differences above
159 2Hz between some individuals in some of the populations (coloured vertical dashed lines, Fig.
160 2A-D). Per population, chimpanzees produced lip-smacks with a mean rhythm of 4.20 Hz at
161 Edinburgh (*P. t. verus* or hybrid, captive), 4.08 Hz at Leipzig (*P. t. verus*, captive), 2.86 Hz at
162 Kanyawara (*P. t. schweinfurthii*, wild) and 1.95 Hz at Waibira (*P. t. schweinfurthii*, wild)
163 (coloured vertical lines, Fig. 2E-J). The average (arithmetic mean) of the mean rhythm per
164 population was 3.27Hz. The mean rhythm between the two captive populations was nearly
165 equal. Between the two wild populations there was an observed difference of ~1Hz. Any dyad
166 with a captive vs. wild population exhibited a difference between >1 and <2.5Hz in lip-smack
167 rhythm. To investigate the apparent differences in the rhythm of lip-smacks between captive
168 vs. wild populations, we ran a generalized linear mixed model with contrasts between the
169 weighted means of the two captive populations and the two wild populations (S2
170 Supplementary Material). The mean average (standard deviation) rhythm peak in captivity was
171 4.69 Hz (± 1.32 Hz) and in the wild was 3.07 Hz (± 0.79 Hz) (corresponding arithmetic average,
172 that is, sum of each population average divided by number of populations, was 4.37 Hz in
173 captivity and 3.09 Hz in the wild), however, we found no difference between groups
174 ($p=0.0866$).

175

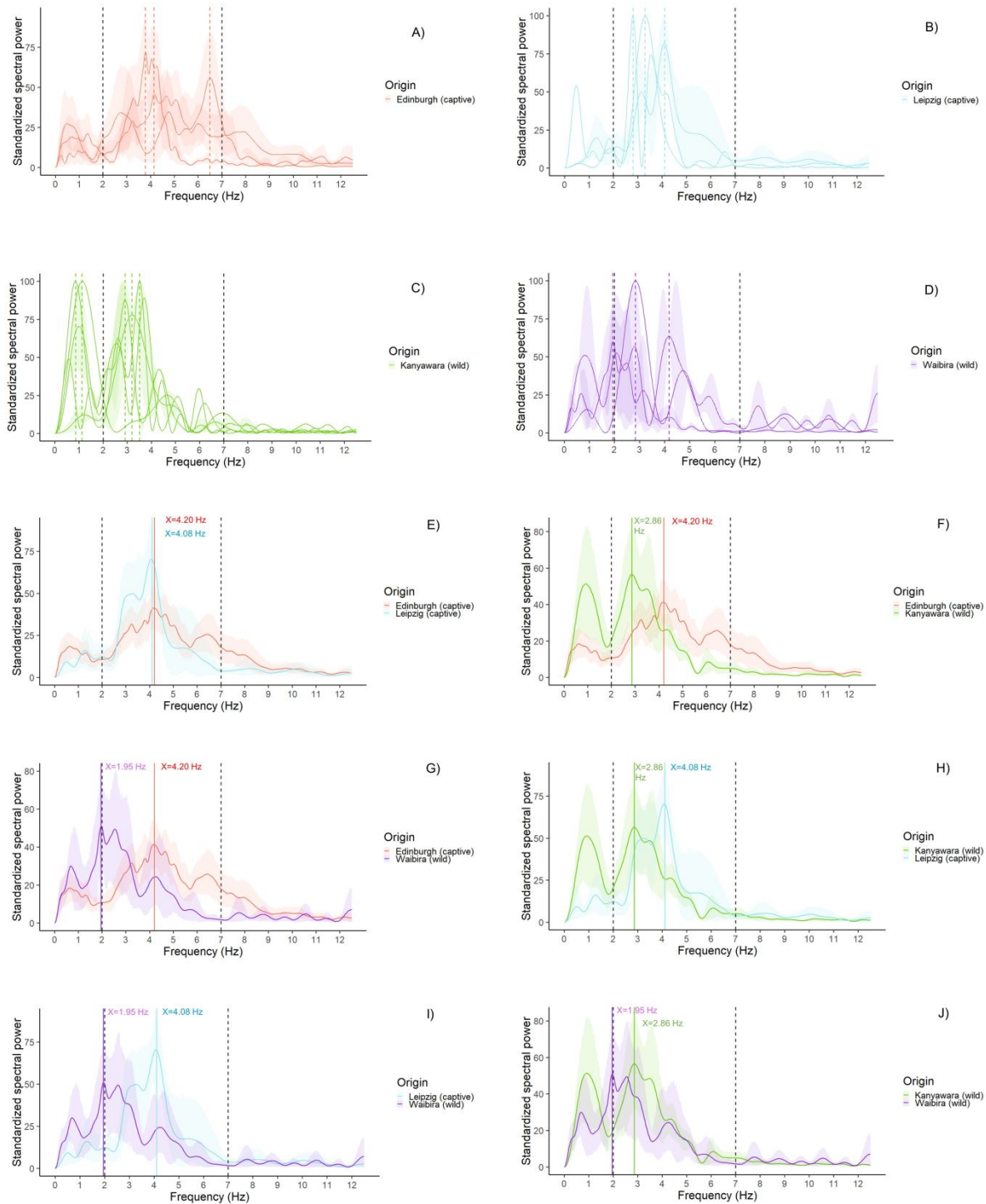


176

177

178 Fig. 1. *Mean standardized power spectral density plot of chimpanzee lip-smacking.* The mean
 179 \pm 95% confidence interval standardized power spectral density plot of all 54 analysed
 180 chimpanzee lip-smack bouts peaks at 4.15 Hz, which represents the dominant frequency of
 181 chimpanzee lip-smack production rate.

182



183

184

185 Fig. 2. Mean standardized power spectral density plot of each individual's lip-smack
186 production rate in each population (A-D) and mean standardized power spectral density plot
187 of each pair of populations (E-J). Shaded areas represent the mean \pm 95% confidence interval
188 standardized power spectral density plot per individual (A-D) and per population (E-J).
189 Coloured dashed vertical lines indicate max frequency peak per individual (A-D) and per
190 population (E-J). Black dashed vertical lines indicate limits of speech-like rhythm frequencies.
191

192 Discussion

193

194 We found that chimpanzees produce lip-smacks at an average speech-like rhythm of 4.15 Hz.
195 These results close the gap between available data on primate fast-paced rhythmic mouth
196 signals and human speech, offering clear support for the hypothesis that speech-rhythm has
197 deep origins within the primate lineage (3, 19, 20) and was built upon existing signal systems
198 (e.g. 26).

199 Our multi-population analyses revealed a level of variation in chimpanzee lip-smack
200 rhythmic production that to our knowledge has not been so far reported in any primate species
201 with similar signals. Differences between individuals and populations reached more than 2Hz
202 at times. Considering that in great apes, the fastest oscillatory vocal signals do not surpass
203 mouth rhythms of 1 Hz (15), the observed variability span in lip-smack production may suggest
204 that these are not hard-wired or stereotypical signals, and/or that socio-ecological factors
205 differently affect lip-smack rhythm by chimpanzees at the level of individuals and/or
206 populations. Despite having pooled for the first-time data across four populations for the
207 analyses of primate fast-paced mouth signals, current sample sizes did not offer adequate
208 statistical power to identify significant differences with confidence or help identify possible
209 correlates. Comparison between captive and wild populations was possible; Despite rhythmic
210 differences of $>1.5\text{Hz}$ between the two types of populations, we found no systematic
211 difference, likely as the result of striking within-population variability and substantial overlap
212 in the range of rhythms present.

213 Alas, despite several primate species being known to exhibit mouth signals at speech-
214 like rhythm, few of the respective studies have disclosed or analysed the levels of variation
215 found between individuals. Although measures of variation in cycle durations (e.g. *SD*) are
216 available (e.g. 12), it is impossible to deduce whether this variation is attributable to intra-
217 individual variation, context or inter-individual variation. Moreover, the lack of multi-site

218 analyses in any of these species prevents a comparison with our results and an interpretation of
219 evidence from a wider phylogenetic or evolutionary angle. Data on variation between
220 individuals and sites would be particularly valuable for gaining new insight into the natural
221 history of primate signals with speech-like rhythm. For example, signals exhibiting speech-like
222 rhythm in macaques and gibbons are generally thought to be innate (27, 28), but orangutan
223 speech-rhythm has been identified in idiosyncratic, species-atypical, individual-specific calls
224 presumed to be learned (15). In our own analyses, there seemed to be variation in the frequency
225 with which individual chimpanzees produced lip-smacks, with some never or only very rarely
226 observed to produce lip-smacks despite similar observation hours as their group members
227 (Hobaiter, unpublished data). Together with the observed degree of variation in lip-smack
228 rhythm across chimpanzee individuals and populations, available great ape data could hint at
229 the intriguing possibility of a fixed-to-flexible transition in the ontogeny of the primate speech-
230 like rhythmic phenotype at the base of the hominid lineage. However, this possibility remains
231 tentative until new, more detailed data become available from both non-hominid and hominid
232 primates. Future research across primate species employing a similar inter-individual and inter-
233 population approach and focusing on prevalence and rhythm variation is critical to discerning
234 the evolutionary trajectory of fast-paced facial movements along the primate lineage,
235 movements that ultimately culminated in the 2-7 Hz rhythm of speech in our species.

236

237

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242

243 Competing Interests

244 The authors declare that they have no conflict of interest.

245

246 Author contributions

247 A.S.P. and E.K. conducted analyses and wrote the paper. C.H. and K.E.S. provided recording
248 materials for video analyses and wrote the paper. A.R.L. conceived the study, conducted
249 analyses and wrote the paper. All authors are accountable for the content and approved the final
250 version of the manuscript.

251

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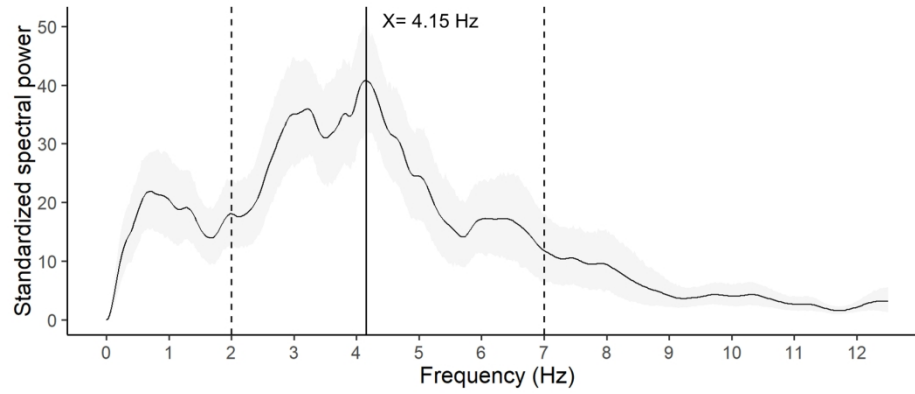
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256 **Bibliography**

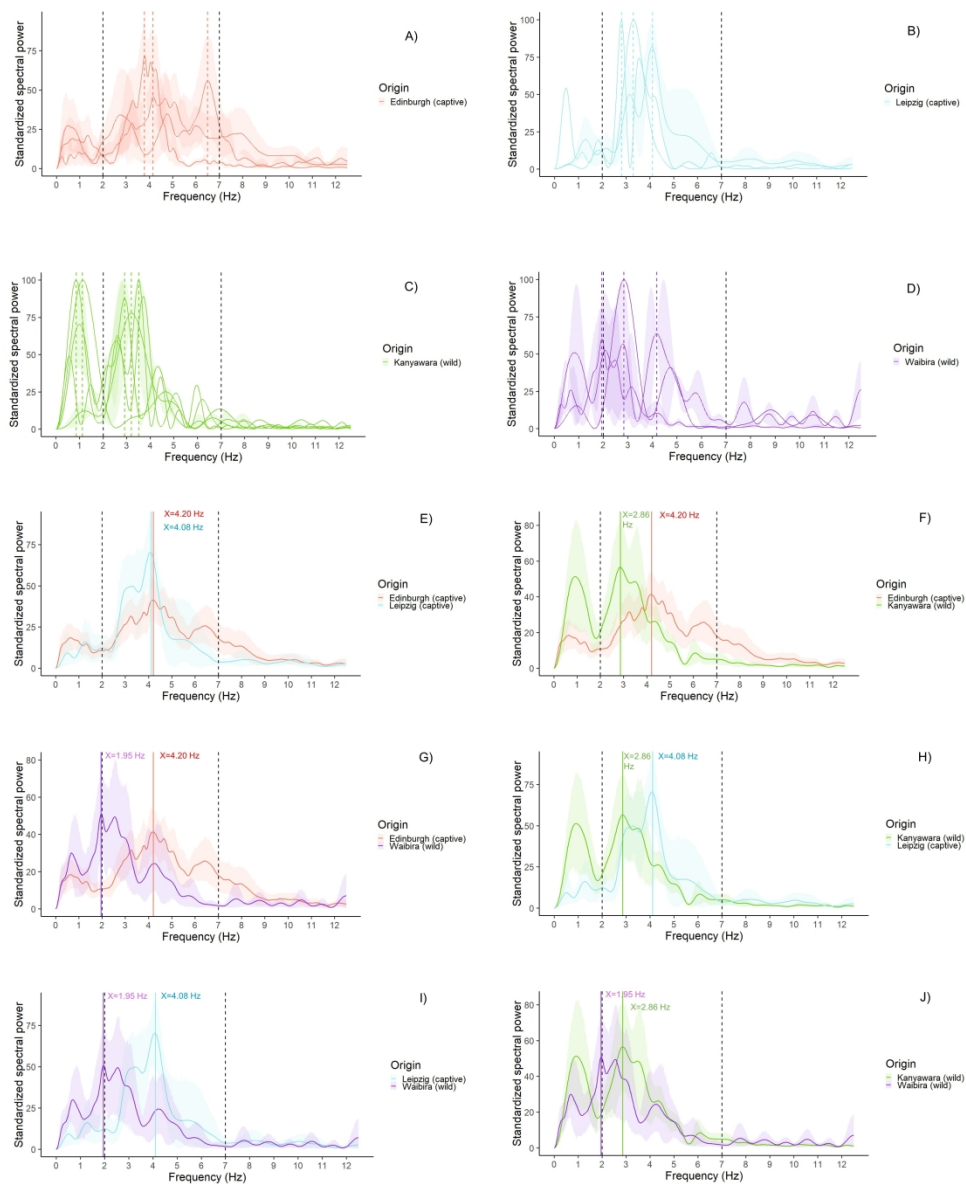
- 257 1. A. R. Lameira, Bidding evidence for primate vocal learning and the cultural substrates
 258 for speech evolution. *Neuroscience & Biobehavioral Reviews* **83**, 429–439 (2017).
- 259 2. T. J. Bergman, J. C. Beehner, M. C. Painter, M. L. Gustison, The speech-like properties
 260 of nonhuman primate vocalizations. *Anim Behav* (2019)
 261 <https://doi.org/10.1016/j.anbehav.2019.02.015>.
- 262 3. A. A. Ghazanfar, D. A. Liao, D. Y. Takahashi, Volition and learning in primate vocal
 263 behaviour. *Anim Behav* (2019) <https://doi.org/10.1016/j.anbehav.2019.01.021>.
- 264 4. L.-J. Boë, *et al.*, Which way to the dawn of speech?: Reanalyzing half a century of
 265 debates and data in light of speech science. *Sci. Adv.* **5**, eaaw3916 (2019).
- 266 5. C. Chandrasekaran, A. Trubanova, S. e bastien Stillittano, A. Caplier, A. A. Ghazanfar,
 267 The natural statistics of audiovisual speech. *PLoS computational biology* **5**, e1000436
 268 (2009).
- 269 6. P. Ladefoged, I. Maddieson, *The Sounds of the World's Languages* (John Wiley {&
 270 Sons, 1996).
- 271 7. P. Ladefoged, S. Disner, *Vowels and Consonants*, 3rd Ed. (Wiley-Blackwell, 2012).
- 272 8. R. Drullman, J. M. Festen, R. Plomp, Effect of reducing slow temporal modulations on
 273 speech reception. *The Journal of the Acoustical Society of America* **95**, 2670–2680
 274 (1994).
- 275 9. T. M. Elliott, F. E. Theunissen, The Modulation Transfer Function for Speech
 276 Intelligibility. *PLoS Comput Biol* **5**, e1000302 (2009).
- 277 10. O. Ghitza, S. Greenberg, On the Possible Role of Brain Rhythms in Speech Perception:
 278 Intelligibility of Time-Compressed Speech with Periodic and Aperiodic Insertions of
 279 Silence. *Phonetica* **66**, 113–126 (2009).
- 280 11. A. A. Ghazanfar, D. Y. Takahashi, N. Mathur, T. W. Fitch, Cineradiography of monkey
 281 lip-smacking reveals putative precursors of speech dynamics. *Current biology : CB* **22**,
 282 1176–1182 (2012).
- 283 12. A. Toyoda, T. Maruhashi, S. Malaivijitnond, H. Koda, Speech-like orofacial oscillations
 284 in stump-tailed macaque (*Macaca arctoides*) facial and vocal signals. *American journal*
 285 *of physical anthropology* **23**, R268 (2017).

- 286 13. T. J. Bergman, Speech-like vocalized lip-smacking in geladas. *Current biology : CB* **23**,
287 R268–R269 (2013).
- 288 14. T. A. Terleph, S. Malaivijitnond, U. Reichard, An analysis of white-handed gibbon male
289 song reveals speech-like phrases. *American journal of physical anthropology* **19**, 252
290 (2018).
- 291 15. A. R. Lameira, *et al.*, Speech-like rhythm in a voiced and voiceless orangutan call. *PLoS*
292 *one* **10**, e116136 (2015).
- 293 16. R. J. Morrill, A. Paukner, P. F. Ferrari, A. A. Ghazanfar, Monkey lipsmacking develops
294 like the human speech rhythm. *Developmental science* **15**, 557–568 (2012).
- 295 17. S. V. Shepherd, W. A. Freiwald, Functional Networks for Social Communication in the
296 Macaque Monkey. *Neuron* **99**, 413–420.e3 (2018).
- 297 18. A. A. Ghazanfar, R. J. Morrill, C. Kayser, Monkeys are perceptually tuned to facial
298 expressions that exhibit a theta-like speech rhythm. *Proceedings of the National*
299 *Academy of Sciences of the United States of America* **110**, 1959–1963 (2013).
- 300 19. A. A. Ghazanfar, D. Y. Takahashi, Facial expressions and the evolution of the speech
301 rhythm. *Journal of cognitive neuroscience* **26**, 1196–1207 (2014).
- 302 20. A. A. Ghazanfar, D. Y. Takahashi, The evolution of speech: vision, rhythm,
303 cooperation. *Trends in cognitive sciences* **18**, 543–553 (2014).
- 304 21. M. PF, The frame/content theory of evolution of speech production. *Behavioral and*
305 *Brain Sciences* **21**, 499–511– discussion 511–46 (1998).
- 306 22. P. Fedurek, K. E. Slocombe, J. A. Hartel, K. Zuberbuhler, Chimpanzee lip-smacking
307 facilitates cooperative behaviour. *Scientific reports* **5**, 13460 (2015).
- 308 23. D. P. Watts, Production of grooming-associated sounds by chimpanzees (Pan
309 troglodytes) at Ngogo: variation, social learning, and possible functions. *Primates*, 1–12
310 (2015).
- 311 24. H. Wickham, *ggplot2: Elegant Graphics for Data Analysis* (Springer-Verlag, 2009).
- 312 25. D. Bates, *lme4: Mixed-effects modeling with R* (2010).
- 313 26. A. R. Lameira, J. Call, Time-space–displaced responses in the orangutan vocal system.
314 *Sci Adv* **4**, eaau3401 (2018).
- 315 27. P. F. Ferrari, *et al.*, Neonatal imitation in rhesus macaques. *PLoS Biol* **4**, e302 (2006).
- 316 28. T. Geissmann, Inheritance of Song Parameters in the Gibbon Song, Analysed in 2
317 Hybrid Gibbons (*Hylobates pileatus* X *H. lar*). *Folia Primatologica* **42**, 216–235 (1984).

318



Mean standardized power spectral density plot of chimpanzee lip-smacking. The mean \pm 95% confidence interval standardized power spectral density plot of all 54 analysed chimpanzee lip-smack bouts peaks at 4.15 Hz, which represents the dominant frequency of chimpanzee lip-smack production rate.



Mean standardized power spectral density plot of each individual's lip-smack production rate in each population (A-D) and mean standardized power spectral density plot of each pair of populations (E-J). Shaded areas represent the mean \pm 95% confidence interval standardized power spectral density plot per individual (A-D) and per population (E-J). Coloured vertical lines indicate max frequency peak for individual (A-D) and per population (E-J). Black dashed vertical lines indicate limits of speech-like rhythm frequencies.

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