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Current Biology

Chimpanzee drumming shows rhythmicity and subspecies variation

Highlights

- Chimpanzees show non-random timing and isochrony in drumming
- Chimpanzee drumming shows key elements of human musical rhythm
- Chimpanzee drumming shows regional (subspecies) variation across diverse ecologies
- Eastern and western chimpanzees have different drumming rhythms

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In brief

Chimpanzees drum on the buttress roots of trees for communication. Eleuteri et al. investigate the presence of key elements of musical rhythm and of regional variation in chimpanzee buttress drumming. They find that, like humans, chimpanzees show non-random timing and isochrony in drumming and that different subspecies drum differently.

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Report

Chimpanzee drumming shows rhythmicity and subspecies variation

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SUMMARY

Rhythmic percussion is present across human cultures and has been proposed as one of the earliest evolved forms of musical expression.[1] Key features of human rhythmic percussion include individual and regional variation, as well as structural features widespread across musical cultures, such as the use of non-random timing and isochrony (i.e., evenly spaced note onsets).[2–5] Comparative studies of drumming in our ape relatives contribute to understanding the evolutionary origins of human rhythmic percussion. In this context, large, diverse datasets allow testing for species-level universals and regional variation. Chimpanzees and bonobos, like humans, drum on instrumental substrates.[2,6–9] Wild chimpanzees drum on resonant tree buttresses, showing individual variation during traveling and resting contexts, and often integrate drumming into their long-distance pant-hoot vocalizations.[6–8] But whether wild chimpanzee drumming shows structural musical features and regional variation in rhythm or in its integration within pant-hoots remains unknown. We show that wild chimpanzees drum with non-random timing and isochrony, providing evidence that rhythmic drumming on instrumental substrates may have been present in our last common ancestor.[2] Furthermore, we found subspecies-level regional rhythmic variation, showing that western chimpanzees drum isochronously, while eastern chimpanzees drum by alternating shorter and longer inter-hit intervals. Western chimpanzees also produce more drumming hits, drum at a faster tempo, and integrate drumming earlier in the pant-hoot vocalization, typically during the rhythmic build-up phase. Chimpanzee buttress drumming shows both species-level structural features of human musicality and stable subspecies regional differences across diverse ecologies.

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RESULTS AND DISCUSSION

Chimpanzees drum on the buttress roots of trees, generating low-frequency sounds and selecting buttresses for their resonating properties.[6,7,9–11] Chimpanzees mainly drum during traveling and resting contexts, where they often combine drumming with pant-hoot vocalizations,[6,7] but they also drum during agonistic displays[9,12] (Figure 1; Audio S1; Videos S1 and S2). The acoustic structure of drumming shows individual variation during traveling and resting but not during agonistic displays, suggesting that chimpanzees can flexibly encode information in drumming for different social functions.[6–8] For example, drumming during traveling and resting seems to be used to transmit information on identity, activity, and location to distant group members potentially to facilitate fission-fusion social dynamics.[6–8]

We investigated 371 drumming bouts produced during traveling and resting[7] by 11 communities in six populations of two chimpanzee subspecies (eastern, *Pan troglodytes schweinfurthii*, *n* = 162; and western, *P.t. verus*, *n* = 209; Figure 2A; Tables S1 and S2) representing the largest cross-site dataset of chimpanzee buttress drumming to date. Drumming bouts were considered sequences of hits produced with hands and/or feet on a buttressed tree.[6] We tested whether chimpanzees drum rhythmically and whether they show regional variation in drumming and in its integration within pant-hoots.

Chimpanzees drum rhythmically and with subspecies rhythms

Non-random timing and isochrony are structural features of musical rhythm found across human cultures.[3–5,14] "Non-random timing" means that musical rhythm consists of events (e.g., hits) structured in time rather than produced randomly.[4,5] Isochrony indicates events separated by intervals of equal duration, like the ticking of a clock.[3,15] Recently, comparative studies revealed these structural features in the vocalizations of different species, including gibbons,[16] lemurs,[17] orangutans,[18] captive chimpanzees,[19] and thrush nightingales.[14] In non-vocal signals, non-random timing and isochrony have been shown in palm cockatoo tool-assisted drumming,[20] in a sustained drumming event by a single captive chimpanzee,[21] and in the motoric behavior of captive chimpanzee agonistic displays.[19] Chimpanzees are our closest living relatives and their drumming has been proposed as homologous to human drumming.[2] But whether wild chimpanzees drum with musical structural features remains unknown.

To test for non-random timing and isochrony in wild chimpanzee drumming bouts, we focused on inter-hit intervals (IHIs), which represent the time elapsed between two adjacent drumming hits. We calculated rhythm ratios (r) between consecutive inter-hit intervals by dividing each inter-hit interval by the sum of itself and the following interval (Table 1; Table S3). We then compared the distribution of these rhythm ratios to a rhythm ratio distribution derived from uniformly random inter-hit intervals (i.e., random distribution; STAR Methods). Across subspecies, all chimpanzees drum with non-random timing (Kolmogorov-Smirnov test, $D = 0.065$, $p < 0.001$). Within subspecies, both western chimpanzees (Kolmogorov-Smirnov test, $D = 0.089$, $p < 0.001$) and eastern chimpanzees (Kolmogorov-Smirnov test, $D = 0.092$, $p < 0.001$) drum with non-random timing. We then compared the two subspecies' rhythm ratio distributions. Western and eastern chimpanzees showed different distributions of rhythm ratios (Kolmogorov-Smirnov test, $D = 0.150$, $p < 0.001$), and visual inspection of these distributions suggested that, while western chimpanzees drum isochronously, eastern chimpanzees drum by alternating shorter and longer inter-hit intervals (Figure 2B).

To assess isochrony, we tested whether the amount of isochronous drumming produced within and across subspecies (i.e., when pooling the subspecies) was higher than the amount of isochronous drumming expected by chance (i.e., in the random distribution; STAR Methods). Within subspecies, western chimpanzees drum *more* isochronously than chance level (median probability difference to chance = 0.053; Wilcoxon signed-rank test, $V = 281$, $p = 0.008$), while eastern chimpanzees drum *less* isochronously than chance level (median probability difference to chance = −0.093; Wilcoxon signed-rank test, $V = 58$, $p = 0.047$; Figures 2B and 2C). Across subspecies, chimpanzees do not drum more or less isochronously than chance level (median probability difference to chance = 0.018; Wilcoxon signed-rank test, $V = 606$, $p = 0.660$), likely due to western chimpanzees drumming *more* while eastern chimpanzees *less* isochronously than chance level. We then compared the use of isochrony and of alternated shorter-longer inter-hit intervals between subspecies. Western chimpanzees drum more isochronously than eastern chimpanzees (median for eastern = 0.111, median for western = 0.257; Wilcoxon signed-rank test for eastern vs. western, $V = 403$, $p = 0.005$; Figure 2C). Conversely, eastern chimpanzees alternate shorter and longer inter-hit intervals more often than western chimpanzees (Welch's t test for lag-one autocorrelations of consecutive inter-hit intervals between subspecies, $t(337.27) = -5.732$, $p < 0.001$; STAR Methods). Supplementary analyses showed that eastern chimpanzees only alternate shorter and longer inter-hit intervals in drumming bouts with three or four hits (Table S4).

Our findings provide the first systematic evidence of non-random timing and isochrony in wild chimpanzee buttress drumming. However, we found no evidence that chimpanzees produce other simple integer ratios widespread in human musical rhythm,[4,14,22] for example 1:2 (an interval followed by one twice its duration) or 1:3 (an interval followed by one three times its duration). In addition to universal features,[3–5,14] human musical rhythm shows regional variation.[14,22,23] While human western rhythms are characterized by simple integer ratios, some African and Balkan musical traditions sometimes use non-simple integer ratios.[14,22,24,25] We also found regional variation at a subspecies level in chimpanzee drumming rhythms: western chimpanzees show isochronous drumming, while eastern chimpanzees drum by alternating shorter and longer inter-hit intervals in drumming bouts with three or four hits (Figure 2B).

A previous study[26] found that, when drumming during agonistic displays, chimpanzees from the Gombe community (Tanzania) produced drumming patterns that aligned with the running gait used to approach the drumming tree, with foot falls landing together as "couplets." The authors suggested that drumming rhythm may thus be constrained by prior gait. Here, when drumming during traveling or resting, eastern chimpanzees sometimes—but not always—drummed with couplets of closely following hits (Figure 2B) and typically drummed after

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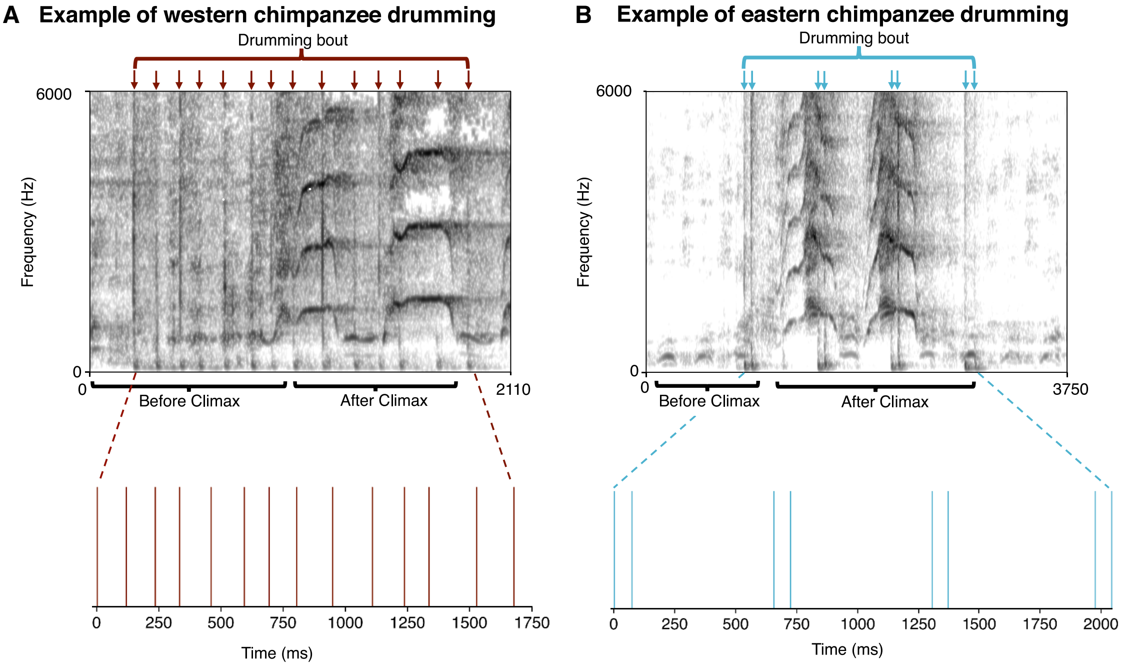

Figure 1. Examples of chimpanzee subspecies' drumming

(A) Example of western chimpanzee drumming. A spectrogram (top) and an event plot (bottom) of a drumming bout produced by a western adult male chimpanzee in the Taï East community in Côte d'Ivoire. The drumming bout consists of 14 hits (highlighted by brown arrows) separated by evenly spaced inter-hit intervals and starts in the build-up phase of the pant-hoot. See corresponding Video S1.

(B) Example of eastern chimpanzee drumming. A spectrogram (top) and an event plot (bottom) of a drumming bout produced by an eastern adult male chimpanzee in the Budongo Sonso community in Uganda. The drumming bout consists of eight hits (highlighted by blue arrows) arranged in an alternation of shorter and longer inter-hit intervals and starts in the build-up phase of the pant-hoot. See corresponding Audio S1 and see Video S2 for another example of eastern drumming. The dotted lines connect the first and last hits of the drumming bout in the spectrograms and event plots.

walking up to or standing next to the tree (V.E. and C.H., personal observation). Our previous study[7] showed variation in display and travel-resting drumming form, and here we show different drumming rhythms in different subspecies. Together, these findings suggest flexibility in drumming structure and that prior gait rhythm is unlikely to fully explain drumming rhythm. Future studies could use detailed pose analysis to assess how locomotory and drumming production mechanics interact together or with buttress characteristics[11] to influence drumming rhythm.

Chimpanzee drumming shows subspecies (regional) variation

Arcadi and colleagues[27] compared the number of hits, the total duration, and the mean inter-hit interval of drumming bouts produced by a Taï chimpanzee community (Côte d'Ivoire) and the Kanyawara community (Uganda) finding no evidence of regional variation. However, in this small dataset the behavioral context of production, which impacts drumming,[7] was not recorded, so the absence of variation may have been due to sampling biases in context. Whether chimpanzee drumming shows regional variation and whether any variation might be due to ecological differences across sites remains unknown.

To test for regional variation in chimpanzee drumming, we used a permuted discriminant function analysis (pDFA[13]) to compare drumming bouts of the 11 communities using the following measures per bout: number of hits, bout duration, variability of all inter-hit intervals (CV), variability between adjacent pairs of inter-hit intervals (normalized pairwise variability index [nPVI]), and entropy of inter-hit intervals (entropy; Table 1; Table S3). Chimpanzee communities varied in their drumming (pDFA observed classification accuracy of 22% where 13% was expected, p = 0.010). Specifically, eastern communities drum differently to western communities, suggesting regional variation at a subspecies level. An additional confirmatory pDFA comparing drumming bouts between subspecies supported subspecies-level regional variation (observed classification accuracy 72% where 54% was expected, p = 0.003).

Generalized linear mixed models (GLMMs[28]) and repeated DFAs (repDFAs[29]) with balanced subsets were used to identify the key variables discriminating groups in the significant pDFAs. nPVI and number of hits were the most contributing variables in both the community and subspecies pDFAs. Specifically, in the community pDFA, nPVI and number of hits loaded highest on discriminant 1 in 798 and 202 out of 1,000 DFAs, respectively (GLMM full-reduced model comparison, nPVI: χ^2_{10} = 29.258, p = 0.001; number of hits: χ^2_{10} = 30.912, p = 0.001; Figure 2D). Bout duration and entropy loaded highest on discriminant 2 in 533 and 345 out of 1,000 DFAs, respectively; however, because the GLMMs were non-significant, they were not considered as key discriminating variables (GLMM full-reduced model comparison, bout duration: χ^2_{10} = 17.735, p = 0.060; entropy: χ^2_{10} = 12.274, p = 0.267). CV loaded highly only on 17 out of 1,000 pDFAs on discriminant 2, showing that the variability of all inter-hit intervals in a drumming bout does not vary across

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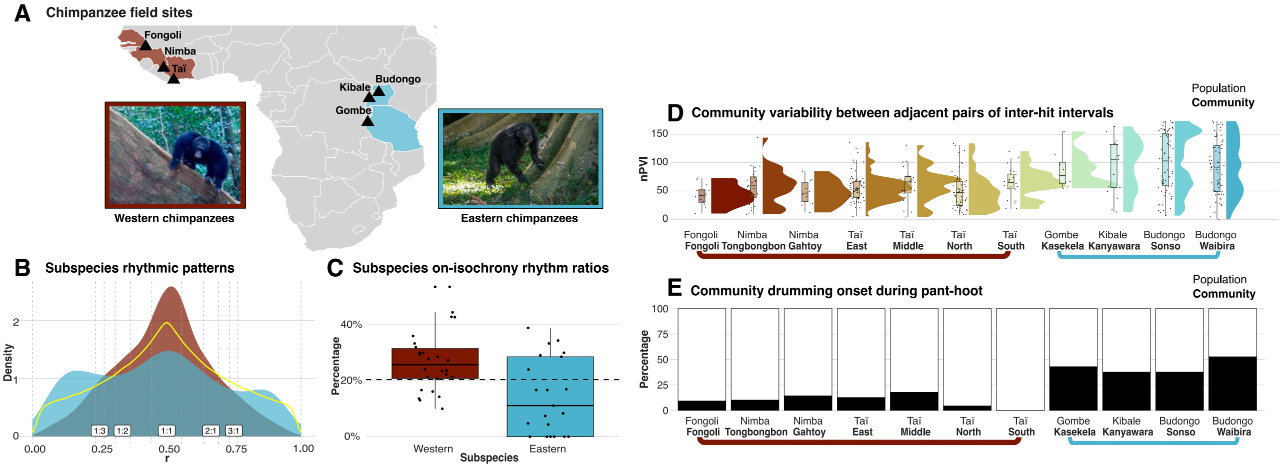

Figure 2. Subspecies (regional) variation in chimpanzee drumming rhythm and integration into pant-hoots

(A) Chimpanzee populations. The locations of the six chimpanzee populations included in the study. The photograph of the eastern chimpanzee is courtesy of coauthor A. Soldati and the photograph of the western chimpanzee is courtesy of K.K.

(B) Subspecies rhythmic patterns. r indicates rhythm ratios of consecutive inter-hit intervals (IHIs) within drumming bouts produced by the two chimpanzee subspecies (n ratios = 1,815; n eastern ratios = 547; n western ratios = 1,268) from n = 371 drumming bouts (n eastern drumming bouts = 162; n western drumming bouts = 209). The yellow line is a simulated distribution of rhythm ratios from a uniform random distribution of inter-hit intervals. Rhythm ratios produced by eastern chimpanzees are indicated in blue; rhythm ratios produced by western chimpanzees are indicated in brown. Both distributions differ significantly from the random distribution and from each other. On-integer ratio ranges are highlighted using dashed lines. The central peak of the western distribution on 1:1 indicates use of isochronous inter-hit intervals (i.e., isochronous drumming), while the peaks at the sides of the eastern distribution indicate the use of alternated shorter and longer inter-hit intervals within drumming bouts.

(C) Subspecies on-isochrony rhythm ratios. Percentage of on-isochrony rhythm ratios of the two subspecies as compared with what would be expected by chance (indicated by the dashed line). In the box plot, the horizontal line shows the median and whiskers indicate the range of values within 1.5 times the interquartile range. The plot shows that western chimpanzees drum more isochronously than chance level, while eastern chimpanzees drum less isochronously than chance level.

(D) Community variability between adjacent pairs of inter-hit intervals. The rain cloud plots contain boxplots, scatterplots, and density distributions of the variability between adjacent pairs of inter-hit intervals (i.e., nPVI) values within drumming bouts (n = 371; n eastern drumming bouts = 162; n western drumming bouts = 209) produced by the 11 chimpanzee communities (four eastern communities and seven western communities). Plots shading from brown to yellow indicate western chimpanzee populations and communities (i.e., Fongoli Fongoli, Nimba Tongbongbon, Nimba Gahtoy, Taï East, Taï Middle, Taï North, and Taï South) while plots shading from light green to blue indicate eastern populations and communities (Gombe Kasekela, Kibale Kanyawara, Budongo Sonso, and Budongo Waibira). In the box plot, the horizontal line shows the median and whiskers indicate the range of values within 1.5 times the interquartile range. nPVI represents the most contributing variable in the community-level pDFA,[13] showing that eastern chimpanzees drum with more variable adjacent pairs of inter-hit intervals than western communities.

(E) Community drumming onset during pant-hoot. The stacked bar plots show the percentage of n = 323 drumming bouts (n eastern drumming bouts = 144; n western drumming bouts = 179) produced by the 11 chimpanzee communities (four eastern communities; seven western communities) accompanied by pant-hoot vocalizations that have their onset before (white) or after (black) the onset of the pant-hoot's climax phase. The plot shows that western chimpanzee communities start drumming later in the pant-hoot than eastern communities, typically during the climax phase.

communities. In the confirmatory subspecies pDFA, only nPVI and number of hits loaded on discriminant 1 in 975 and 25 out of 1,000 DFAs, respectively (GLMM full-reduced model comparison, nPVI: $\chi^2_1 = 25.617$, $p < 0.001$; number of hits: $\chi^2_1 = 19.198$, $p < 0.001$; eastern: median = 4; mode = 3; western: median = 7; mode = 5; Figure 3). Specifically, western chimpanzees drum with more hits and with less variable adjacent inter-hit intervals than eastern chimpanzees (Figures 2D and 3A).

As our data spanned 24 years, we further tested the stability of the five drumming measures across time within subspecies (STAR methods; Table 1). Subspecies drumming remained stable across time (GLMM full-reduced model comparisons, nPVI: $\chi^2_1 = 0.580$, $p = 0.446$; CV: $\chi^2_1 = 1.050$, $p = 0.305$; entropy, $\chi^2_1 = 0.446$, $p = 0.504$; number of hits, $\chi^2_1 = 1.489$, $p = 0.222$).

To summarize, while the total variability of inter-hit intervals (CV) within drumming bouts did not vary between subspecies, the variability between adjacent pairs of inter-hit intervals varied (nPVI, Figure 2D). In other words, chimpanzee subspecies use the same building blocks to produce different drumming rhythms. This structuring may represent a parallel with human music: across cultures, fewer than five durational values are typically used to produce rhythmic patterns and different arrangements of similar intervals produce different rhythms (e.g., baroque vs. reggae).[4] Additionally, western chimpanzees produce drumming bouts with more hits than eastern chimpanzees, but of the same duration, suggesting that western chimpanzees drum with a faster tempo (Figure 3). A supplementary GLMM comparing drumming tempo in the two subspecies confirmed this finding (GLMM full-reduced model comparison, tempo: $\chi^2_1 = 11.463$, $p = 0.001$). Compared with human rhythmic drumming, chimpanzees across subspecies drum with fewer hits and show a faster average inter-hit interval of 229 ms (human tapping average IHI: 600 ms)[5,30] (Table S3). Human drumming contains more hits than chimpanzee drumming; however, human music consists of looped rhythms and events (e.g., hits) grouped into twos and threes.[4,5] By showing rhythmic elements in chimpanzee drumming, we contribute to

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Table 1. Drumming measures

Measure	Description
Number of hits	Number of hits in a drumming bout
Bout duration	Duration of a drumming bout measured from the center of the first hit in the bout to the center of the last hit in the bout. Measured in seconds
Coefficient of variation of inter-hit intervals (CV)	Rhythmic measure of variability of all inter-hit intervals[a] in a drumming bout relative to the mean inter-hit interval in the bout. Lower values indicate lower variability. Measure calculated at the level of the drumming bout
Variability between adjacent pairs of inter-hit intervals (nPVI)	Rhythmic measure of variability (i.e., durational contrast) between adjacent pairs of inter-hit intervals in a drumming bout. Lower values indicate lower adjacent inter-hit interval variability. The maximum value the nPVI can have is 200. Measure calculated at the level of the drumming bout
Shannon's entropy (entropy)	Rhythmic measure of structuredness of a drumming bout. Entropy was used to measure how predictable durations of inter-hit intervals within drumming bouts are. First, we used a k-means clustering algorithm to identify categories of inter-hit intervals (k) based on their duration; k was determined separately for each individual chimpanzee by comparing the performance of the clustering using silhouette scores, which quantify the performance of the clustering algorithm. The clustering fit was best when the number of categories (k) was either two (defined as "short" and "long") or three (short, "medium," and long) depending on the individual. Using more than three categories did not improve silhouette scores for any individual. Next, we calculated Shannon's entropy using the counts of inter-hit intervals in each durational category for each drumming bout. A bout's entropy is lowest when one can predict with high certainty what a hypothetical new inter-hit interval would be as in, for example, the case of a drumming bout containing only short inter-hit intervals. In this case one can be relatively confident that a hypothetical new inter-hit interval will also be a short inter-hit interval. Entropy is highest when it is difficult to predict what a hypothetical new inter-hit interval would be, as in the case of a bout containing an equal number of short, medium, and long inter-hit intervals. In this case one cannot be confident about the duration of a new, hypothetical, inter-hit interval in that bout. Measure calculated at the level of the drumming bout
Rhythm ratios (r)	Rhythmic measure to explore the presence of rhythmic patterns of inter-hit intervals within drumming bouts. Calculated by dividing each inter-hit interval (IHI_k) by itself plus the following interval (IHI_{k+1}): $r_k = \frac{IHI_k}{IHI_k + IHI_{k+1}}$. Measure calculated at the level of the inter-hit interval

Measures computed to examine the structure of drumming bouts produced by chimpanzees. See Table S3 for descriptive statistics of the drumming measures.

[a] Inter-hit interval (IHI)—latency between two consecutive hits measured from the center of the first hit to the center of the second hit.

understanding the building blocks that may have preceded sustained rhythmic drumming in humans.

Within and across subspecies, the populations sampled live in diverse habitats ranging from primary and secondary forest to savanna mosaic. To test whether ecology impacts chimpanzee drumming, we compared drumming bouts across the six populations using the five drumming measures (Table 1). Chimpanzee drumming did not vary among all sampled populations (all populations pDFA observed classification accuracy of 25% where 19% was expected, $p = 0.102$). This lack of variation across populations suggests that large-scale ecological differences between populations' habitats does not affect chimpanzee drumming. As the populations belong to different subspecies, we further assessed whether ecology affects drumming while controlling for subspecies variation by comparing populations *within* each subspecies. Chimpanzee drumming did not vary between populations of the same subspecies living in different habitats (western populations pDFA, observed classification accuracy of 59% where 58% was expected, $p = 0.401$; eastern populations pDFA, observed classification accuracy of 35% where 37% was expected, $p = 0.542$).

Taken together, our results suggest that subspecies differences, rather than ecological factors, likely drive regional variation in chimpanzee drumming. However, future studies should directly investigate whether specific ecological variables (e.g., territory size, tree species, or geometric properties[11]) influence chimpanzee drumming.

Chimpanzee pant-hoot and drumming combinations show subspecies (regional) variation

Arcadi and colleagues[27] found population variation in the combination of drumming and pant-hoot vocalizations: Taï chimpanzees incorporated drumming earlier in the pant-hoot, typically during the build-up phase, while Kanyawara chimpanzees usually started drumming during the climax. To test for systematic regional variation in chimpanzee drumming behavior, we compared when chimpanzees started drumming during the pant-hoot across communities and across populations. At both community and population level, chimpanzees started drumming at different points during the pant-hoot (GLMM full-reduced model comparing communities, $\chi^2_9 = 18.663$, $p = 0.028$; GLMM full-reduced model

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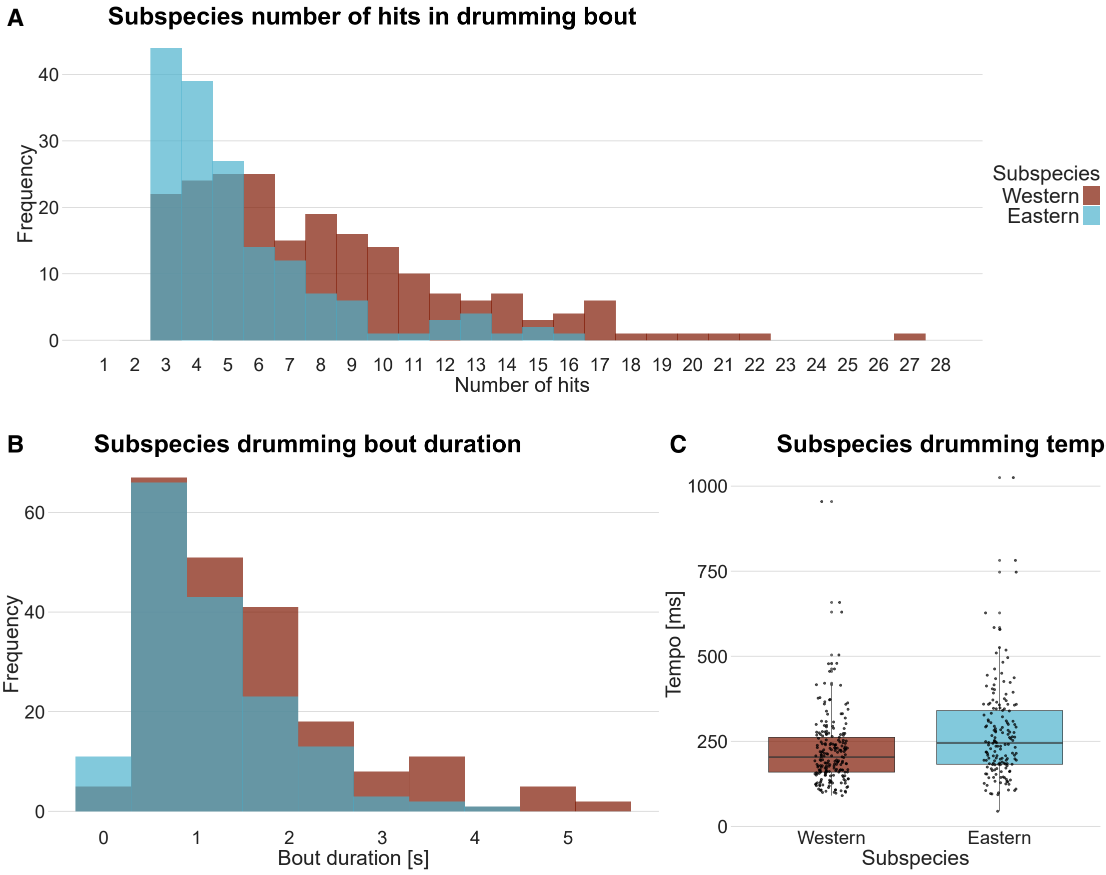

Figure 3. Subspecies (regional) variation in chimpanzee drumming hits and tempo

(A) Subspecies drumming number of hits. The plot shows histograms of the number of hits within drumming bouts. Number of hits represented a highly contributing variable in the pDFA, revealing that western chimpanzee (in brown) drum with more hits (median = 7; mode = 5) within drumming bouts than eastern chimpanzees (in blue; median = 4; mode = 3).

(B) Subspecies drumming bout duration. The plot shows histograms of the drumming bout duration, which was not a highly contributing variable in the subspecies pDFA, suggesting subspecies do not vary in drumming bout duration.

(C) Subspecies drumming tempo. The plot shows boxplots of drumming tempo revealing that western chimpanzees drum with a faster tempo than eastern chimpanzees. In all plots the drumming bouts were produced by the two chimpanzee subspecies (*n* drumming bouts = 371; *n* eastern drumming bouts = 162; *n* western drumming bouts = 209).

comparing populations, $\chi^2_5 = 14.640$, $p = 0.012$). Specifically, across both communities and populations, western chimpanzees are more likely to start drumming before, rather than after, the onset of the pant-hoot climax, typically during the build-up (Figure 2E).[27] A confirmatory GLMM comparing subspecies supported subspecies-level regional variation (GLMM full-reduced model comparing subspecies, $\chi^2_1 = 14.380$, $p < 0.001$).

The build-up phase of the pant-hoot consists of repeated inhalations and exhalations, which show isochronous-like rhythm.[19] Western chimpanzees may start drumming during build-ups as it may be easier to integrate their isochronous drumming during an isochronous vocal phase than during climax screams.

Potential social drivers of drumming subspecies variation

Our findings show that subspecies differences, rather than ecological differences, likely shape regional variation in chimpanzee drumming. Chimpanzee party sizes seem constrained by food availability[31,32] and remain relatively stable across communities of different sizes.[33,34] Because western females are more gregarious and range more often across the entire home range than eastern females,[35–37] western chimpanzees are more likely to regularly encounter more community members, fostering greater overall social cohesion than in eastern communities. Western communities are less aggressive toward outgroups than their eastern counterparts, as evidenced by the rarity of lethal inter-community encounters in western chimpanzees compared with its regular occurrence in eastern chimpanzees.[38,39] These subspecies differences in sociality may potentially explain regional variation in drumming behavior. Patterns of variable interval lengths have the potential for greater expressivity than isochronous patterns, where the same interval length is repeated.[15] If eastern chimpanzees are socially dispersed more often, exhibiting more diverse adjacent inter-hit intervals within drumming (Figure 2D) could provide greater flexibility to transmit social information relevant to locating distant group members. Pant-hoot climaxes carry identity information across large distances.[40] Being more often dispersed, eastern chimpanzees might integrate drumming—which can be heard further away than pant-hoots[41]—during climaxes more often than western chimpanzees to facilitate individual recognition over large distances. Future research should investigate whether (1) as in humans, higher isochrony in western chimpanzees is associated with more synchronized behavior (i.e., joint pant-hooting or drumming) that may promote cohesion and coordination[15]; (2) eastern chimpanzees show more diverse adjacent inter-hit intervals within drumming to convey variable information related to fission or fusion events; (3) eastern chimpanzees possess stronger individual or community signatures than western chimpanzees to aid in regulating fission-fusion and inter-community social dynamics; (4) the regional variation represents a neutral evolved cultural difference.

Conclusions

We show stable subspecies-level regional differences in the structure of chimpanzee drumming and in its integration within pant-hoots, despite substantial ecological variation across chimpanzee sites. We provide evidence of some musical structural features in the drumming behavior of our closest living relatives, suggesting that rhythmic percussion on instrumental substrates might have been present before humans and chimpanzees diverged approximately 7–9 mya.[2] Our findings highlight percussive behavior in non-human apes as a promising system for exploring the evolution of musicality.

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to the lead contact, Vesta Eleuteri: vesta.eleuteri@univie.ac.at.

Materials availability

This study did not generate any new reagents or animal lines.

Data and code availability

- All data have been deposited and are publicly available at Zenodo: https://doi.org/10.5281/zenodo.15175482.
- All original code has been deposited and is publicly available at Zenodo: https://doi.org/10.5281/zenodo.15175482.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

V.E., original draft; V.E., C.H., J.v.d.W., and A.R., conceptualization; V.E., W. W., A. Soldati, C.C., N.D., P.F., K.E.G., K.K., M.F., L.S., H.D.C., G.M., and C. H., data collection; C.C., K.K., L.S., K.S., J.P., M.L.W., R.M.W., K.Z., and C. H., access to field sites or supervision of data collection; V.E. and W.W., data coding; V.E., data curation; V.E. and J.v.d.W., formal analysis; C.H. and A.R., study supervision; C.H., A. Stoeger, and A.R., funding. All authors were involved in reviewing and editing.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Subjects and study sites
  - Ethical note
- METHOD DETAILS
  - Data collection
  - Eastern chimpanzees
  - Western chimpanzees
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Acoustic analyses
  - Drumming measures
  - Statistical analyses

SUPPLEMENTAL INFORMATION

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REFERENCES

1. Morley, I. (2013). The Prehistory of Music: Human Evolution, Archaeology, and the Origins of Musicality (Oxford University Press). https://doi.org/10.1093/acprof:osobl/9780199234080.001.0001.
2. Fitch, W.T. (2011). The biology and evolution of rhythm: unravelling a paradox. In Language and Music as Cognitive Systems, P. Rebuschat, M. Rohmeier, J.A. Hawkins, and I. Cross, eds. (Oxford University Press), pp. 73–95. https://doi.org/10.1093/acprof:oso/9780199553426.003.0009.
3. Ravignani, A., and Madison, G. (2017). The Paradox of Isochrony in the Evolution of Human Rhythm. Front. Psychol. *8*, 1820. https://doi.org/10.3389/fpsyg.2017.01820.
4. Savage, P.E., Brown, S., Sakai, E., and Currie, T.E. (2015). Statistical universals reveal the structures and functions of human music. Proc. Natl. Acad. Sci. USA *112*, 8987–8992. https://doi.org/10.1073/pnas.1414495112.
5. Ravignani, A., Delgado, T., and Kirby, S. (2016). Musical evolution in the lab exhibits rhythmic universals. Nat. Hum. Behav. *1*, 0007. https://doi.org/10.1038/s41562-016-0007.

Please cite this article in press as: Eleuteri et al., Chimpanzee drumming shows rhythmicity and subspecies variation, Current Biology (2025), https://doi.org/10.1016/j.cub.2025.04.019

6. Arcadi, A.C., Robert, D., and Boesch, C. (1998). Buttress drumming by wild chimpanzees: temporal patterning, phrase integration into loud calls, and preliminary evidence for individual distinctiveness. Primates *39*, 505–518. https://doi.org/10.1007/BF02557572.
7. Eleuteri, V., Henderson, M., Soldati, A., Badihi, G., Zuberbühler, K., and Hobaiter, C. (2022). The form and function of chimpanzee buttress drumming. Anim. Behav. *192*, 189–205. https://doi.org/10.1016/j.anbehav.2022.07.013.
8. Babiszewska, M., Schel, A.M., Wilke, C., and Slocombe, K.E. (2015). Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (Pan troglodytes). Am. J. Phys. Anthropol. *156*, 125–134. https://doi.org/10.1002/ajpa.22634.
9. Goodall, J. (1986). The Chimpanzees of Gombe: Patterns of Behavior (Cambridge University Press).
10. Fitzgerald, M., Willems, E.P., Gaspard Soumah, A., Matsuzawa, T., and Koops, K. (2022). To drum or not to drum: Selectivity in tree buttress drumming by chimpanzees (Pan troglodytes verus) in the Nimba Mountains, Guinea. Am. J. Primatol. *84*, e23382. https://doi.org/10.1002/ajp.23382.
11. Wilhelm, W., Eleuteri, V., Koops, K., Fitzgerald, M., Zuberbühler, K., and Hobaiter, C. (2025). Selectivity in buttress drumming tree properties among chimpanzees (Pan troglodytes schweinfurthii) of the Waibira community in Budongo Forest, Uganda. Am. J. Primatol. *87*, e23712. https://doi.org/10.1002/ajp.23712.
12. Soldati, A., Fedurek, P., Dezecache, G., Call, J., and Zuberbühler, K. (2022). Audience sensitivity in chimpanzee display pant hoots. Anim. Behav. *190*, 23–40. https://doi.org/10.1016/j.anbehav.2022.05.010.
13. Mundry, R., and Sommer, C. (2007). Discriminant function analysis with nonindependent data: consequences and an alternative. Anim. Behav. *74*, 965–976. https://doi.org/10.1016/j.anbehav.2006.12.028.
14. Roeske, T.C., Tchernichovski, O., Poeppel, D., and Jacoby, N. (2020). Categorical Rhythms Are Shared between Songbirds and Humans. Curr. Biol. *30*, 3544–3555.e6. https://doi.org/10.1016/j.cub.2020.06.072.
15. Merker, B.H., Madison, G.S., and Eckerdal, P. (2009). On the role and origin of isochrony in human rhythmic entrainment. Cortex *45*, 4–17. https://doi.org/10.1016/j.cortex.2008.06.011.
16. Raimondi, T., Di Panfilo, G., Pasquali, M., Zarantonello, M., Favaro, L., Savini, T., Gamba, M., and Ravignani, A. (2023). Isochrony and rhythmic interaction in ape duetting. Proc. Biol. Sci. *290*, 20222244. https://doi.org/10.1098/rspb.2022.2244.
17. De Gregorio, C., Valente, D., Raimondi, T., Torti, V., Miaretsoa, L., Friard, O., Giacoma, C., Ravignani, A., and Gamba, M. (2021). Categorical rhythms in a singing primate. Curr. Biol. *31*, R1379–R1380. https://doi.org/10.1016/j.cub.2021.09.032.
18. Lameira, A.R., Hardus, M.E., Ravignani, A., Raimondi, T., and Gamba, M. (2024). Recursive self-embedded vocal motifs in wild orangutans. eLife *12*, RP88348. https://doi.org/10.7554/eLife.88348.
19. van der Vleuten, B.J.R., Hovenkamp, V.A., Varkevisser, J.M., and Spierings, M.J. (2024). Context-dependent rhythmicity in chimpanzee displays. Proc. Biol. Sci. *291*, 20242200. https://doi.org/10.1098/rspb.2024.2200.
20. Heinsohn, R., Zdenek, C.N., Cunningham, R.B., Endler, J.A., and Langmore, N.E. (2017). Tool-assisted rhythmic drumming in palm cockatoos shares key elements of human instrumental music. Sci. Adv. *3*, e1602399. https://doi.org/10.1126/sciadv.1602399.
21. Dufour, V., Poulin, N., Curé, C., and Sterck, E.H.M. (2015). Chimpanzee drumming: a spontaneous performance with characteristics of human musical drumming. Sci. Rep. *5*, 11320. https://doi.org/10.1038/srep11320.
22. Jacoby, N., Polak, R., Grahn, J.A., Cameron, D.J., Lee, K.M., Godoy, R., Undurraga, E.A., Huanca, T., Thalwitzer, T., Doumbia, N., et al. (2024). Commonality and variation in mental representations of music revealed by a cross-cultural comparison of rhythm priors in 15 countries. Nat. Hum. Behav. *8*, 846–877. https://doi.org/10.1038/s41562-023-01800-9.
23. Savage, P.E. (2022). An Overview of Cross-Cultural Music Corpus Studies. In The Oxford Handbook of Music and Corpus Studies, D. Shanahan, J.A. Burgoyne, and I. Quinn, eds. (Oxford University Press). https://doi.org/10.1093/oxfordhb/9780190945442.013.34.
24. Polak, R., and London, J. (2014). Timing and Meter in Mande Drumming from Mali. Music Theor. Online *20*. https://doi.org/10.30535/mto.20.1.1.
25. Polak, R. (2010). Rhythmic Feel as Meter: Non-Isochronous Beat Subdivision in Jembe Music from Mali. Music Theor. Online *16*. https://doi.org/10.30535/mto.16.4.4.
26. Arcadi, A.C., and Wallauer, W. (2013). They Wallop Like They Gallop: Audiovisual Analysis Reveals the Influence of Gait on Buttress Drumming by Wild Chimpanzees (Pan troglodytes). Int. J. Primatol. *34*, 194–215. https://doi.org/10.1007/s10764-013-9656-1.
27. Clark Arcadi, A., Robert, D., and Mugurusi, F. (2004). A comparison of buttress drumming by male chimpanzees from two populations. Primates *45*, 135–139. https://doi.org/10.1007/s10329-003-0070-8.
28. Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., and White, J.-S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. *24*, 127–135. https://doi.org/10.1016/j.tree.2008.10.008.
29. Neumann, C. (2022). repDFA: repeated DFAs with balanced subsets. https://rdrr.io/github/gobbios/cfp/man/repDFA.html.
30. London, J. (2012). Hearing in Time: Psychological Aspects of Musical Meter (Oxford University Press). https://doi.org/10.1093/acprof:oso/9780199744374.001.0001.
31. Itoh, N., and Nishida, T. (2007). Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. Primates *48*, 87–96. https://doi.org/10.1007/s10329-006-0031-0.
32. Newton-Fisher, N.E., Reynolds, V., and Plumptre, A.J. (2000). Food Supply and Chimpanzee (Pan troglodytes schweinfurthii) Party Size in the Budongo Forest Reserve, Uganda. Int. J. Primatol. *21*, 613–628. https://doi.org/10.1023/A:1005561203763.
33. Badihi, G., Bodden, K., Zuberbühler, K., Samuni, L., and Hobaiter, C. (2022). Flexibility in the social structure of male chimpanzees (Pan troglodytes schweinfurthii) in the Budongo Forest, Uganda. R. Soc. Open Sci. *9*, 220904. https://doi.org/10.1098/rsos.220904.
34. Koops, K., Akankwasa, W., Camara, H.D., Fitzgerald, M., Keir, A., Mamy, G., Matsuzawa, T., Péter, H., Vicent, K., Zuberbühler, K., et al. (2024). Flexible grouping patterns in a western and eastern chimpanzee community. Am. J. Primatol. *86*, e23593. https://doi.org/10.1002/ajp.23593.
35. Lehmann, J., and Boesch, C. (2005). Bisexually bonded ranging in chimpanzees (Pan troglodytes verus). Behav. Ecol. Sociobiol. *57*, 525–535. https://doi.org/10.1007/s00265-004-0891-5.
36. Lehmann, J., and Boesch, C. (2008). Sexual Differences in Chimpanzee Sociality. Int. J. Primatol. *29*, 65–81. https://doi.org/10.1007/s10764-007-9230-9.
37. Wakefield, M.L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. Anim. Behav. *85*, 1303–1313. https://doi.org/10.1016/j.anbehav.2013.03.019.
38. Wilson, M.L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I.C., Hashimoto, C., Hobaiter, C.L., Hohmann, G., Itoh, N., Koops, K., et al. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. Nature *513*, 414–417. https://doi.org/10.1038/nature13727.
39. Muller, M.N., and Wrangham, R.W. (2004). Dominance, aggression and testosterone in wild chimpanzees: a test of the ‘challenge hypothesis’. Anim. Behav. *67*, 113–123. https://doi.org/10.1016/j.anbehav.2003.03.013.
40. Fedurek, P., Zuberbühler, K., and Dahl, C.D. (2016). Sequential information in a great ape utterance. Sci. Rep. *6*, 38226. https://doi.org/10.1038/srep38226.
41. Boesch, C. (1991). Symbolic communication in wild chimpanzees? Hum. Evol. *6*, 81–89. https://doi.org/10.1007/BF02435610.

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42. Reynolds, V. (1965). Chimpanzees of the Budongo forest. Primate Behav. 368–424.
43. Thompson, M.E., Muller, M.N., Machanda, Z.P., Otali, E., and Wrangham, R.W. (2020). The Kibale Chimpanzee Project: Over thirty years of research, conservation, and change. Biol. Conserv. *252*, 108857. https://doi.org/10.1016/j.biocon.2020.108857.
44. Goodall, J. (1986). The Chimpanzees of Gombe: Patterns of Behavior (Harvard University Press).
45. Boesch, C., and Boesch-Achermann, H. (2000). The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution (Oxford University Press). https://doi.org/10.1093/oso/9780198505082.001.0001.
46. Koops, K. (2011). Chimpanzees in the Seringbara Region of the Nimba Mountains. In The Chimpanzees of Bossou and Nimba, T. Matsuzawa, T. Humle, and Y. Sugiyama, eds. (Springer), pp. 277–287. https://doi.org/10.1007/978-4-431-53921-6_29.
47. Pruetz, J.D., Bertolani, P., Ontl, K.B., Lindshield, S., Shelley, M., and Wessling, E.G. (2015). New evidence on the tool-assisted hunting exhibited by chimpanzees (Pan troglodytes verus) in a savannah habitat at Fongoli, Sénégal. R. Soc. Open Sci. *2*, 140507. https://doi.org/10.1098/rsos.140507.
48. Hobaiter, C., Badihi, G., Daly, G.B. de M., Eleuteri, V., Graham, K.E., Grund, C., Henderson, M., Rodrigues, E.D., Safryghin, A., Soldati, A., et al. (2021) The Great Ape Dictionary video database. Version 1.0.0. Zenodo. https://doi.org/10.5281/zenodo.5600472.
49. Fedurek, P., Donnellan, E., and Slocombe, K.E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. Behav. Ecol. Sociobiol. *68*, 1345–1355. https://doi.org/10.1007/s00265-014-1745-4.
50. Mitani, J.C., and Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. Anim. Behav. *45*, 735–746. https://doi.org/10.1006/anbe.1993.1088.
51. Arcadi, A.C. (1996). Phrase structure of wild chimpanzee pant hoots: Patterns of production and interpopulation variability. Am. J. Primatol. *39*, 159–178. https://doi.org/10.1002/(SICI)1098-2345(1996)39:3<159::AID-AJP2>3.0.CO;2-Y.
52. Shannon, C.E. (1948). A mathematical theory of communication. Bell Syst. Tech. J. *27*, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.
53. van der Werff, J., Ravignani, A., and Jadoul, Y. (2024). thebeat: A Python package for working with rhythms and other temporal sequences. Behav. Res. Methods *56*, 3725–3736. https://doi.org/10.3758/s13428-023-02334-8.
54. Jadoul, Y., Tufarelli, T., Coissac, C., Gamba, M., and Ravignani, A. (2025). Hidden assumptions of integer ratio analyses in bioacoustics and music. Preprint at arXiv. https://doi.org/10.48550/arXiv.2502.04464.
55. Vorberg, D., and Wing, A. (1996). Modeling variability and dependence in timing. Chapter 4. In Handbook of Perception and Action Motor Skills, H. Heuer, and S.W. Keele, eds. (Academic Press), pp. 181–262. https://doi.org/10.1016/S1874-5822(06)80007-1.
56. Agresti, A. (2012). Categorical Data Analysis (John Wiley & Sons).
57. Desai, N.P., Fedurek, P., Slocombe, K.E., and Wilson, M.L. (2022). Chimpanzee pant-hoots encode individual information more reliably than group differences. Am. J. Primatol. *84*, e23430. https://doi.org/10.1002/ajp.23430.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data	This paper	https://zenodo.org/records/15175482
Example videos	This paper	Videos S1 and S2
Example audios	This paper	Audio S1
Experimental models: Organisms/strains		
Chimpanzees (*Pan troglodytes* spec.)	Budongo Central Forest Reserve, Uganda; Kibale National Park, Uganda; Gombe National Park, Tanzania; Taï National Park, Ivory Coast; Seringbara study site, Nimba Mountains, Guinea; Fongoli study site, Senegal	N/A
Software and algorithms		
Praat	Paul Boersma and David Weenink	https://www.fon.hum.uva.nl/praat/
Python	Python Software Foundation	https://www.python.org
R	R foundation	https://www.r-project.org/
Thebeat	Jelle van der Werff, Andrea Ravignani, Yannick Jadoul	https://thebeat.readthedocs.io

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subjects and study sites

We collected data on buttress drumming in 11 chimpanzee communities across six populations of two subspecies (eastern, *Pan troglodytes schweinfurthii* and western, *Pan troglodytes verus*) of chimpanzees between 1999 and 2023.

East Africa

The Sonso and Waibira communities of the Budongo population inhabit the Budongo Central Forest Reserve in western Uganda, a 793 km^2 reserve containing 482 km^2 of medium-altitude and semi-deciduous tropical secondary forest.[42] The Kanyawara community of the Kibale population inhabits the Kibale National Park in western Uganda, a 766km^2 mid-altitude forest containing a mosaic of primary forest, logged forest, grassland, and swamp.[43] The Kasekela community of the Gombe population inhabits the Gombe National Park in western Tanzania, a small 35km^2 forest located along the shore of Lake Tanganyika on a mountainous landscape consisting of an evergreen and semi-deciduous forest on the lower slopes and a mosaic of thicket, woodland, and grassland on the upper slopes.[44]

West Africa

The North, East, Middle, and South communities of the Taï population inhabit the Taï National Park in Côte d'Ivoire, a 4540 km^2 evergreen and low-altitude primary forest.[45] The Gahtoy and Tongbongbon communities of the Nimba population inhabit the Nimba Mountains in the Republic of Guinea, which cover approximately 175 km^2 of wet, montane primary forest including rocky peaks, rough cliffs, steep river valleys, and high-altitude savannah.[10,46] The Fongoli community of the Fongoli population lives in a woodland-savannah habitat in south-eastern Senegal. The vegetation in Fongoli is a mosaic of woodland, grassland, bamboo, and gallery forest, with closed habitats covering less than 5% of the range.[47]

Ethical note

Data collection across sites followed the ASAB guidelines for the treatment of animals in behavioural studies (2018). Ethical approval for the study was given by the School of Psychology and Neuroscience of the University of St Andrews Animal Welfare Ethics Committee on the 5th of May 2019. We followed the ASAB guidelines for the treatment of animals in behavioural research and teaching (ANIMAL BEHAVIOUR, 135, I-X). Data collection conformed to the Code of Best Practices for Field Primatology established by the International Primatological Society (2014).

METHOD DETAILS

Data collection

We considered buttress drumming (hereafter drumming) as any percussive behaviour produced with hands and/or feet on the flange-like buttress roots that support tree trunks.[6,44] Following Arcadi,[6] a drumming bout was defined as a sequence of hits produced by a chimpanzee striking the buttress roots of one tree with hands and/or feet.

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Eastern chimpanzees

Drumming bouts were collected in the Budongo Forest in Uganda from the Budongo Waibira community by VE between June 2019 and March 2020, by WW between June and July 2023, and extracted from archival video data from 2017 and 2019[48]; and from the Budongo Sonso community by ASoldati between October 2018 and March 2020 and extracted from archival video data from 2011 and 2021.[48] Drumming bouts were collected in the Kibale National Park in Uganda from the Kibale Kanyawara community by PF between October 2010 and July 2011. Drumming bouts were collected in the Gombe National Park in Tanzania from the Gombe Kaseleka community by Nasibu Zuberi Madumbi and Hashim Issa Salala supervised by ND and MW between May and October 2017.

Western chimpanzees

Drumming bouts were collected in the Taï National Park in Côte d'Ivoire from the Taï Middle and Taï North communities by CC between February 1999 and May 2000 and from the Taï East and Taï South communities by LS between October 2013 and January 2015 and by CH between January and February 2020. Drumming bouts were collected at the Seringbara study site in the Nimba Mountains in Guinea from the Nimba Tongbongbon community by KK, MF, and a team of research assistants and staff between February 2012 and May 2022; and from the Nimba Gahtoy community by KK, MF, and a team of research assistants and staff between January 2020 and April 2022. Drumming bouts were collected in the Fongoli study site in Senegal from the Fongoli community by KEG between May and June 2023.

In all communities drumming bouts were collected or extracted from long-term data with an *ad libitum* sampling approach. For each drumming bout we noted information on the signaller identity and the behavioural context of production of the drumming behaviour as: feeding, displaying, travelling, or resting. Feeding: the signaller drummed when feeding on the ground or when arriving at a feeding tree. Displaying: the signaller drummed when displaying with piloerection, and throwing objects, charging, gesturing, or calling, when other chimpanzees were nearby. Travelling: the signaller drummed when locomoting through the forest to find distant resources or group members (note that locomotion solely to reach the drumming tree was not considered as travelling; and for cases where the signaller was resting immediately before or after travelling, we considered the context as travelling). Resting: the signaller was on the ground and was not engaging in any of the activities above.

In Budongo Waibira drumming behaviour was filmed and recorded with a Sennheiser MKE 400 directional microphone (audio sample rate: 44.1 kHz, resolution: 16 bits per sample) mounted on a Panasonic HC-V700 video-camera. In Budongo Sonso drumming behaviour was recorded with a directional microphone Sennheiser MKH 416 with Marantz PMD661 MkII solid-state recorder (audio sample rate: 44.1 kHz, resolution: 32 bits per sample). In Kibale Kanyawara drumming behaviour was recorded with a Marantz Professional PMD661 solid state recorder and a Sennheiser ME67 directional microphone (audio sample rate: 44.1 kHz, resolution: 32 bits per sample). In Gombe Kasekela drumming behaviour was recorded with a Sennheiser ME66 shotgun microphone with K6 power module and a Marantz PMD661 MKII audio recorder (audio sample rate: 96 kHz, resolution: 16 bits per sample). In Taï Middle, Taï North, and Taï South drumming behaviour was recorded with a Sennheiser ME65/K6 directional microphone (frequency response: 50-15,000 Hz ± 2.5 dB re 20 lPa) and a Sony WMD6C Professional Walkman or Marantz PMD 222 cassette recorder, or with different Panasonic video-camera models (e.g., HC-V720, HC-V785, HC-VX1). In Taï East drumming behaviour was recorded with different Panasonic video-camera models (e.g., HC-V720, HC-V785, HC-VX1). In Nimba Tongbongbon and Nimba Gahtoy drumming behaviour was recorded with Browning Recon Force Elite HP4 and Bushnell Trophy Cam (various models) motion-triggered cameras. In Fongoli drumming behaviour was recorded with a Panasonic HC-VX1 video-camera. Video recordings were converted with Wondershare UniConverter Software 10.5.0 to WAV audio files to conduct acoustic analyses.

QUANTIFICATION AND STATISTICAL ANALYSIS

Acoustic analyses

We conducted acoustic analyses in Praat version 6.1.54 only on drumming bouts produced by adult male chimpanzees, as data available from female chimpanzees were generally scarce and not present in some communities. For acoustic analyses we annotated only drumming bouts in which all drumming hits could be clearly visually discriminated in spectrograms. We annotated the start and end of the drumming bout and the timing of each hit within the bout at its centre (i.e., halfway in time; following Eleuteri et al.[7]). Pant-hoots are the species-typical loud vocalizations used by chimpanzees to maintain contact with conspecifics and can be composed of up to four subsequent phases: the "introduction" (low "hoo" elements), the "build-up" (low intensity voiced inhaled and exhaled elements), the "climax" (high-intensity and high-frequency loud voiced elements resembling screams), and the "let-down" (a low-intensity final element).[40,49–51] For drumming bouts produced during pant-hoots, we also annotated the start and end of the pant-hoot and of each of the pant-hoot phases: introduction, build-up, climax, let-down.[40,51] Acoustic analyses were conducted by VE and WW.

Inter-rater reliability was calculated on 36 randomly selected samples coded by VE and recoded by a trained coder (WW) on the drumming variables: number of hits, bout duration; and the pant-hoot variables: start phase and end phase. We found substantial to almost perfect reliability on all variables (weighted Cohen's kappa for number of hits, k = 0.707, z = 7.42, $p < 0.001$; intra-class correlation coefficient for bout duration, r = 0.83, F(35, 31.7) = 11.5, $p < 0.001$; weighted Cohen's kappa for start phase, k = 0.806, z = 5.39, $p < 0.001$; weighted Cohen's kappa for end phase, k = 0.863, z = 7.66, $p < 0.001$). The original data coded by VE were included in the statistical analyses.

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Drumming measures

Previous studies have suggested that drumming serves different functions in different behavioural contexts. During agonistic displays drumming may be used by chimpanzees to target immediate or nearby audiences with impressive visual and audible behaviour.[12,44] During resting and travelling drumming may be used to communicate the signaller's identity and location to distant group members, possibly to coordinate fission-fusion events, similarly to pant-hoot vocalizations.[7,8,44,51] Because we recorded and annotated too few drumming bouts in the context of feeding to conduct any statistical analyses, we only included drumming bouts produced during travelling and resting contexts (following Eleuteri et al.[7]). To ensure that the drumming styles of individuals were representative of community styles, we only included communities with at least two individuals who each contributed at least three drumming bouts comprising at least three hits. Drumming bouts with fewer than three hits (corresponding to two inter-hit intervals) were excluded because rhythm ratios are calculated for subsequent intervals (see below).

To represent the structure of buttress drumming for each drumming bout included we computed five measures: number of hits, bout duration, coefficient of variation of all inter-hit intervals (CV), variability between adjacent pairs of inter-hit intervals (nPVI: normalised pairwise variability index), and Shannon's entropy of inter-hit intervals (entropy[52]; Table 1; Table S3). In addition, to test for the presence of non-random timing and isochrony of inter-hit intervals within the drumming bouts, we computed so-called rhythm ratios (r) of consecutive inter-hit intervals by dividing each inter-hit interval (IHI) by its duration plus the duration of the following inter-hit interval (following Roeske et al.[14] and De Gregorio et al.[17]; see below for statistical analyses). Measures were only computed for individual chimpanzees who contributed, across all drumming bouts, at least 10 hits (i.e., 9 inter-hit intervals) to ensure sufficient variation in the inter-hit intervals for entropy and rhythm ratios calculations. CV, nPVI, and entropy measures were extracted using the *thebeat*[53] package in Python (Table 1).

Statistical analyses

Do chimpanzees drum rhythmically?

To test for musical rhythmic properties in chimpanzee drumming, we built on the methodology used by previous studies.[14,17,18] For each individual chimpanzee, we first split the rhythm ratios into histogram bins (i.e., ranges of ratios). Following Roeske et al.,[14] bins were centred on on-integer ratios and off-integer ratios. On-integer bins (highlighted in Figure 2B with dashed lines) were centred around the integer ratios typical of human musical rhythm.[14,17,18] The following on-integer rhythm ratios were used: 1:3 (bin centre: 0.25) representing a ratio between an interval and its consecutive interval three times its duration; 1:2 (bin centre: 0.33) representing a ratio between an interval and its consecutive interval twice its duration; 1:1 (bin centre: 0.50) representing a ratio between two consecutive intervals of equal duration (i.e., isochronous bin); 2:1 (bin centre: 0.66) representing a ratio between an interval and its consecutive interval half its duration; and 3:1 (bin centre: 0.75) representing a ratio between an interval and its consecutive interval one-third its duration. The bins in-between these integer ratios represent the off-integer bins. After defining the bins, we calculated the bin counts for each individual chimpanzee. For more information on bin selection, see.[14,17]

To test whether, across and within subspecies, chimpanzees drum with non-random timing, we simulated a random uniform distribution of inter-hit intervals (IHIs) with the durations of the minimum and maximum observed inter-hit intervals in our dataset as left and right bounds.[14,17] We then applied the equation used to compute the rhythm ratios presented in Table 1 to calculate rhythm ratios for the random uniform distribution of IHIs. Subsequently, we compared the distributions of the rhythm ratios of all chimpanzees together and of the two subspecies separately to the distribution of rhythm ratios of the random uniform distribution of IHIs (i.e., random distribution) using Kolmogorov-Smirnov tests. We also tested for the presence of different rhythmic patterns in eastern and western chimpanzees by comparing the distributions of their rhythm ratios using another Kolmogorov-Smirnov test, and by visually inspecting the presence of any specific rhythmic patterns within plots of the distributions.

Recently, the issue has been raised by Jadoul et al.[54] that normalization procedures used in previous studies[14,17,18] implicitly—and in our case, wrongly—assume a null hypothesis of uniformly distributed rhythm ratios. The actual null hypothesis is usually that the rhythm ratios are distributed according to the random distribution presented in Figure 2B, which results from sampling intervals (and not rhythm ratios) from a uniform random distribution. The previously used normalization procedure involved dividing the number of observations in each histogram bin by the width of that bin on the x axis. This procedure can lead to an overestimation of observed isochronous rhythm ratios as compared to chance level when intervals are randomly sampled from a uniform distribution. Based on the recommendations by Jadoul et al.,[54] we devised a method to test for the presence of isochrony that avoids this overestimation, and used it to compare the amount of isochrony between subspecies, and to compare the amount of isochrony to chance level. First, we counted how many of an individual chimpanzee's rhythm ratios fell into the isochronous bin (i.e., 1:1), and compared that to the total number of observed rhythm ratios for that individual (i.e. $\frac{number\ of\ isochronous\ ratios}{total\ number\ of\ ratios}$). This value represented the empirical probability of a rhythm ratio falling into the isochronous bin for each individual. Then, we computed the corresponding value for what would be expected by chance, i.e. the mathematical probability of a rhythm ratio falling into the isochronous bin when intervals are sampled from a random uniform distribution. This mathematical probability was calculated using the formula provided in Jadoul et al.,[54] which yielded a probability for the isochronous bin of 0.204. To compare the empirical probabilities of isochronous drumming to the expected (mathematical) probability we used one-sample Wilcoxon signed-rank tests: one for all chimpanzees together and two for each subspecies (eastern and western) separately. A final Wilcoxon signed-rank test was used to compare the amount of isochronous drumming in the two subspecies.

Lastly, we confirmed the different use of alternated shorter-longer inter-hit intervals in the two subspecies (Figure 2B) by comparing lag-one autocorrelations of consecutive inter-hit intervals produced by eastern and western chimpanzees. A negative lag-one

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autocorrelation indicates alternation of shorter and longer inter-hit intervals within drumming bouts (cf. Vorberg and Wing[55]). We included in the analyses n = 1815 ratios (n eastern ratios = 547; n western ratios = 1268) from n = 371 drumming bouts (n eastern drumming bouts = 162; n western drumming bouts = 209) with at least three hits recorded in the contexts of travelling and resting by 47 individuals (21 eastern and 26 western) from 11 communities (four eastern and seven western) across six populations (three eastern and three western) of two subspecies (eastern, *Pan troglodytes schweinfurthii* and western, *Pan troglodytes verus*; Tables S1 and S2).

Human musical rhythms are typically longer than the three-hit or four-hit drumming bouts we included in our dataset.[4,5] We therefore conducted supplementary analyses including drumming bouts with at least five hits (Table S4). We included here n = 1363 ratios (n eastern ratios = 352; n western ratios = 1011) from n = 204 drumming bouts (n eastern drumming bouts = 64; n western drumming bouts = 140). Our results here differed to those in our main analysis in that eastern chimpanzees do not drum differently to random and that they do not drum *less* isochronously than expected by chance and by alternating shorter and longer inter-hit intervals. However, here our sample size for Eastern chimpanzees (n = 352) is almost half the sample size of the full dataset (n = 547) and may have thus led to loss of statistical power. We also conducted supplementary analyses fully replicating previous studies (e.g. ref. Roeske et al.,[14] De Gregorio et al.,[17] and Lameira et al.[18]; Table S5).

Do chimpanzees from different regions drum differently?

To test for the presence of regional variation in chimpanzee drumming and for the effect of ecology on drumming, we compared drumming bouts of different communities and of different populations using, respectively, two nested permuted discriminant function analyses (pDFA[13] with 1000 permutations: randomised data sets including the original dataset). We used pDFAs because our data violated the assumption of independence for discriminant function analysis, as some of the drumming bouts were produced by the same individual chimpanzees. pDFA allowed us to address the violation of independence using a permutation approach, and to test whether the observed classification accuracy of a discriminant function analysis (DFA[56]) is significantly higher than expected by chance, while accounting for the accuracy inflating effect of a confounding factor (in our case: individual). In the two pDFAs we included individual as the control factor, and community and population as test factors, respectively. In both pDFAs we entered as variables the drumming measures: number of hits, bout duration, nPVI, CV, and entropy (Tables 1 and S3). Variables that achieved a more symmetrical distribution after log transformation were log transformed (in our data: number of hits, bout duration). In the analysis we included a total of n = 371 drumming bouts (n eastern drumming bouts = 162; n western drumming bouts = 209) with at least three hits recorded in the contexts of travelling and resting by 47 individuals (21 eastern individuals; 26 western individuals) from 11 communities (four eastern individuals; seven western individuals) across six populations (three eastern populations; three western populations) of two subspecies (eastern and western; Tables S1 and S2). Following Desai et al.,[57] we used repeated DFAs with balanced subsets (repDFA) and generalized linear mixed models (GLMMs[28]) to identify the key variables discriminating the test factor in significant pDFAs. First, we used the repDFA function to create 1000 balanced datasets in a crossed design and to run 1000 DFAs reporting the variables with the highest coefficient on the linear discriminant functions in each DFA. We then used GLMMs to test the significance of the variables with the highest coefficients in most DFAs. We controlled for individual by including it as a random effect. The pDFAs were conducted using the R function and instructions provided by Roger Mundry[13] and the repDFA was performed using a function by Christof Neuman,[29] subsequently modified by Desai et al.[57]

Our drumming data spanned a total period of 24 years. To test whether drumming remains stable throughout time within subspecies, we used five GLMMs. We included as predictor the interaction between subspecies and the number of days passed from the first date of data collection until the 1st of January 2024. The response variables in the five GLMMs were the five drumming measures: number of hits, bout duration, CV, nPVI, and entropy (Table 1). We again controlled for individual by including it as a random effect.

Do chimpanzees from different regions start drumming at different points during pant-hoot vocalizations?

Lastly, to further address regional variation in chimpanzee drumming behaviour, we tested whether communities and populations start drumming at different points during the pant-hoot using two GLMMs with a binomial error structure.[28] The response variable for both GLMMs indicated whether the drumming bout started before or after the onset of the climax phase of the pant-hoot (“before climax start” = 1; “after climax start” = 0). The predictors were, respectively, community and population, and we controlled for individual by entering it as a random effect. Out of n = 371 drumming bouts, a total of n = 356 (96%, of which n = 159 (98%) by eastern chimpanzees and n = 197 (94%) by western chimpanzees) were produced with a pant-hoot; n = 9 (0.02%) were produced without a pant-hoot, and for n = 8 (0.02%) it was unknown if a pant-hoot was produced. Drumming bouts starting in the pause between the pant-hoot phases, that were produced after the pant-hoot, or where the pant-hoot phase was unclear were removed from analyses. Taï South was removed from the GLMM as the community had no drumming bouts starting after the onset of the climax. The final dataset included in the analyses consisted of n = 302 drumming bouts (n eastern drumming bouts = 144; n western drumming bouts = 158) produced in the contexts of travelling and resting by 42 individuals (21 eastern individuals; 21 western individuals) from 10 communities (four eastern communities; six western communities) of six populations (three eastern populations; three western populations) of two subspecies (eastern and western; Tables S1 and S2). All analyses and plots were conducted in R version 4.3.1.