Coupled whole-body rhythmic entrainment between two chimpanzees

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Dance is an icon of human expression. Despite astounding diversity around the world’s cultures and dazzling abundance of reminiscent animal systems, the evolution of dance in the human clade remains obscure. Dance requires individuals to interactively synchronize their whole-body tempo to their partner’s, with near-perfect precision. This capacity is motorically-heavy, engaging multiple neural circuitries, but also dependent on an acute socio-emotional bond between partners. Hitherto, these factors helped explain why no dance forms were present amongst nonhuman primates. Critically, evidence for conjoined full-body rhythmic entrainment in great apes that could help reconstruct possible proto-stages of human dance is still lacking. Here, we report an endogenously-effected case of ritualized dance-like behaviour between two captive chimpanzees – synchronized bipedalism.

We submitted video recordings to rigorous time-series analysis and circular statistics. We found that individual step tempo was within the genus’ range of “solo” bipedalism. Between-individual analyses, however, revealed that synchronisation between individuals was non-random, predictable, phase concordant, maintained with instantaneous centi-second precision and jointly regulated, with individuals also taking turns as “pace-makers”. No function was apparent besides the behaviour’s putative positive social affiliation. Our analyses show a first case of spontaneous whole-body entrainment between two ape peers, thus providing tentative empirical evidence for phylogenies of human dance. Human proto-dance, we argue, may have been rooted in mechanisms of social cohesion among small groups that might have granted stress-releasing benefits via gait-synchrony and mutual-touch. An external sound/musical beat may have been initially uninvolved. We discuss dance evolution as driven by ecologically-, socially- and/or culturally-imposed “captivity”.

Dance is one of the richest facets of human expression. A staggering abundance of forms can be found across the world’s cultures (UNESCO Intangible Cultural Heritage List), together with a plethora of mesmerizing analogous performances across the animal world1–6. Yet, there seem to exist no parallel behaviours among our closest relatives, the (nonhuman) great apes, calling into question how and why this trait emerged within the terminal branch of our phylogenetic tree and subsequently evolved so expansively7–9.

Dance, as a human social event, is propped on rhythmic entrainment – the capacity of (at least) two individuals to synchronize with instantaneous precision to a shared and steady rhythm, characteristically manifested through whole-body movement. Whether seen as an evolutionary by-product, or adaptation to promote social cohesion for religion or war, speculation abounds on possible scenarios for the emergence of rhythmic entrainment in the human clade. Despite a burgeoning science of music evolution10 and the recent formulation of testable frameworks about the evolution of dance11, understanding the proto-stages of dance in the human lineage hinges on what may be learned from primate comparative research and meticulous analyses of rhythm and synchrony12.

However, the evidence gathered thus far within the primate order does not paint a coherent picture of how dance evolution may have played out13. For example, experimental studies with monkeys and great apes have focused on rhythmic synchronization primed by humans under dedicated training-protocols where subjects did not engage with conspecifics14,15. In natural or naturalistic conditions, nonhuman primates engage in rhythmic

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behaviours\cite{16-19}, some of which can be compared, at a purely mechanical level, with the use of music instruments\cite{20,21}. Analyses of these behaviours have been seldom done in light of dance evolution and rarely adopted accurate measures of rhythm and synchrony, with only a few exceptions in the field\cite{22}. Critically, there is a lack of examples in great apes with obvious social and whole-body components that could establish a direct parallel with rhythm entrainment as observed in human dance. Do (or can) our closest relatives engage in dance-like behaviours at all? Only in the presence of such putative examples may evolutionary hypotheses be sensibly formulated about the form and function of dance precursors in the human clade.

Here, we present the first evidence for co-synced rhythmic entrainment between two great apes in a naturalistic environment. Holly and Bahkahri, two captive chimpanzees (\textit{Pan troglodytes}) at St Louis Zoo (Missouri, USA), engaged in coupled bipedalism, one following the other in near contact, similarly to a Conga line in humans (Fig. 1, see Supplemental Material for video links).

**Methods**

**Study subjects.** Chimpanzees were recorded at the Saint Louis Zoological Park, Missouri, United States. Holly (Studbook ID 1064) and Bahkahri (1065) performed the behaviour occupying at all times the same relative position to each other during synchronous bipedalism, with Holly in the front and Bahkahri in the back. The two females have the same age and were both born in 1998 with two weeks apart, although at different zoos. Both were transferred to the St Louis Zoo, with one day apart in that same year, when they were less than 4 months old. The mothers accompanied neither transfer. The behaviour exhibited by Holly and Bahkahri may have developed at the St Louis Zoo, where the two females have lived throughout virtually all their lives, although the exact timing of the behaviour’s inception is uncertain and could precede their arrival at the zoo. At the time of writing, they share the enclosure with 6 other chimpanzees, with an outside area of several thousands of square foot space surrounded by rocky cliffs, offering different climbing structures and composed by vegetation types providing a naturalistic setting similar to the natural habitats where chimpanzees occur in the wild.

The zoo displayed chimpanzee entertainment shows until 1982 when it ceased such performances as an expression of its ethical concerns and priority towards chimpanzee conservation and welfare. The development of the behaviour in Holly and Bahkahri was not, therefore, the result of human training by caretakers or staff as they arrived at the zoo 16 years later after such performances ceased.

**Data collection.** As in previous related work\cite{5}, data were collected from videos posted on the global database \textit{www.youtube.com}. Videos were searched using the terms “conga line,” “chimpanzees,” and/or “St Louis”. Twenty-three videos were found and spanned from October 2011 and April 2015 (see Supplementary Materials). All videos were uploaded at different dates and from different users. Videos were recorded at a resolution of 30 frames/second as indicated by Youtube advanced settings. No videos recorded the same event (e.g. from different angles), which was verified either by the position and direction of the subjects in their enclosure or by the background noise during the recordings. All videos were recorded behind enclosure windows.

These data were publicly recorded opportunistically based on non-continuous observations and were not the result of a video-screening or data-mining exercise by the authors. Accordingly, the number of bouts observed is presumed to represent a far underestimation of the actual frequency of the behaviour. It can be deduced from the available material that individuals engaged in the behaviour at least up to four times in one day (i.e. four bouts of the behaviour were recorded on the same date). We do not describe incidental moments when two chimpanzees moved together and at the same time, but instead a conspicuous behavior.

**Data analysis.** Behavioural coding was conducted using Cowlog web version\cite{23}. One of the authors coded the moment of foot-ground contact for each bipedal step for both individuals, setting frame speed to slow motion, namely between 1 and 5 frames/second. Coding was done based on direct observation of foot motion.

**Figure 1.** Illustration of the two chimpanzee subjects performing synchronous bipedalism (by ARL).
or individuals’ gait at leg and shoulder height. The reliability of the annotations was assessed by having a second coder annotating seven random bouts containing 366 steps. The median difference in onset timings between the annotators was 0.05 s (SD = 0.076 s), and this error was normally distributed (17.9, p < 0.001 in Anderson-Darling test of normality), suggesting that the discrepancies were small, random, and approximately the duration of one video frame (0.0417 s).

The statistical analyses were conducted with R24 using the circular25 and vars26 packages. For temporal dynamics analysis, the discrete step times were converted into time-series at 100 Hz sampling rate and filtered with third-order non-causal, Butterworth filter for maximal clarity. The annotated timing data (raw data, Fig. S1) is available as Supplementary Material File.

**Ethics statement.** This study complied with ethical guidelines and good research conduct for image-only analyses of videos publicly deposited in YouTube. Human subjects were neither involved in this study nor portrayed in any of the analysed videos. No information was used for analyses about any human person, social media user or social media behaviour. This study has in no manner reused or distributed these videos. No copyright or copyright infringement has been intended in this study.

**Results**

**Qualitative description of the behaviour.** The individual initiating synchronous bipedalism, either front or hind, cued the other through gesture or posture. Occasionally they began rocking their upper body while sitting (commonly out of phase) before starting the behaviour. By the first or second step individuals were in phase and synchronous. Synchrony was maintained even when walking over large obstacles, such as a fallen log, or when making a turn of 180°. Synchronous bipedal walk was progressive, i.e., individuals always covered some distance with each step. Individuals typically collected some object before engaging in the behaviour, namely a blanket or bundle of straw. The front individual held objects with both hands, whereas the hind individual used only her right hand while maintaining contact with the front individual with her left hand. Individuals were always within few centimeters from each other. Individuals occasionally paused the behaviour and resumed it, taking with them the same objects in the same original direction. In one occasion individuals performed the behaviour without holding objects and objects seemed available throughout the enclosure, without an obvious function of transport. On this occasion, the front individual presented a quadrupedal gait primarily, while the hind individual made dorsoventral contact with the front individual. No interference from other individuals was observed.

**Quantitative analyses of the behaviour.** For the analysed data, average bout duration of synchronous bipedalism between the two chimpanzees was 24.6 s (minimum = 2.62 s, maximum = 47.84 s, SD = 20.1 s, Fig. S1). Because in various cases the recordings did not encompass the complete behaviour bout, this figure should be taken as a possible lower bound. The two chimpanzees exhibited a mean step duration (tempo) of 0.89 s (Fig. 2A,B), ranging from 0.81 and 1.49 seconds mean tempo per bout (N bout = 28). Standard deviation of step duration for front and hind individuals was 0.154 s and 0.152 s, respectively. This bipedal gait was slower than that recorded in the wild [0.81 s, t(391) = 10.56, p < 0.001]27 and faster than gait tempo in captivity [1.21 s, t(391) = −38.84, p < 0.001]28 in the genus Pan. This behaviour was, therefore, overall within the range of typical bipedal walking pace performed by single individuals.

Auto-correlation analysis (focusing on 0.5–1.5 s range) on the time series of individual step patterns yielded a maximal autocorrelation at 0.89 s across all bouts for both chimps (Fig. 2B), but maximum period varied across bouts (median = 0.90 s, SD = 0.055 s, Fig. S2). A cross-correlation analysis (from −0.5 to +0.5 seconds in 1/24 video frame increments) between the time-series from both individuals showed a maximum lag of 0 s across all bouts (Fig. 2C), even though a relative minor variation occurred across bouts at the millisecond scale (mean cross-correlation maximum = 0.0014 s, SD = 0.008 s, Fig. S3). These results indicate that the individuals were constant in tempo.

To investigate the consistency of step periods for both individuals, the periods were analysed concerning the angle of step in reference to the mean step period (period = 360° = 0.89 s, where the first step was set 0° angle) using circular statistics. The mean angle for the individuals was close to 0° (1.7°, SD constant in tempo.

cross-correlation maximum

all bouts (Fig. 2C), even though a relative minor variation occurred across bouts at the millisecond scale (mean

video frame increments) between the time-series from both individuals showed a maximum lag of 0 s across all bouts for both individuals, Fig. 2D). Neither of these distributions were uniform (Rayleigh test < 0.001, Fig. 2D). The peaks expressed as angles across the common period also exhibited a significant correlation (rS = 0.939, p < 0.001, bootstrapped CI95% = 0.905–0.972). These results corroborate that subjects always maintained synchrony even though their exact body cadence exhibited different subtleties.

There was no significant overall difference between the individuals in step period using circular analysis of variance [F(1,1292) = 0.004, p = 0.95], although the bouts themselves exhibited a significant difference [F(27,1296) = 9.55, p < 0.001]. These results indicate that the chimpanzees always maintained synchrony regardless their rhythmic pace.

Granger causality analyses with optimal lag (0.28 s, determined by Akaike criterion within vector autoregression across lags 0 to 0.3 s) suggested that the front chimpanzee predicted the hind chimpanzee at the p < 0.05 level in 9 bouts, whereas the reverse was true in 10 bouts. In the remaining 19 bouts there was a two-way causal relation between individuals. Thus, there was no consistent leading role, and both individuals may have interleaved the role of the pacemaker.

Rhythmic synchronization comprised the holding of objects (i.e. straw bundles), but no directed transport or object manipulation was apparent (see Supplemental Material), substantiating the behaviour’s idiosyncrasy.
Discussion

Time series analysis and circular statistics provide evidence of self-elicited rhythmic entrainment between two chimpanzees involving whole-body engagement. This behaviour has been hitherto undescribed in primates outside human dance, hence potentially shedding new light on the potential primitive forms and functions of proto-dance expression within the human clade. Subjects exhibited a gait movement that was individually regular and mutually synchronized, demonstrating joint rhythm keeping. Whenever one individual accelerated or decelerated her pace, her partner matched her pace. Both individuals alternatively took the role of pace-keeper, but in other occasions the rhythm was kept in a two-way fashion without one of the individuals taking a statistically-identifiable leading role. Rhythmic entrainment was also dynamic between the two chimpanzees. That is, they kept rhythmic entrainment across a range of different tempos and irrespectively of the absolute pace of their gait movement.

Our analyses rule out the possibility that the two chimpanzees engaged in synchronous bipedalism by sheer chance. The simple independent tallying of one individual performing bipedal gait after the other could not have resulted in rhythmic entrainment with instant centisecond precision on a consistent basis across different pace speeds and across years, as reported here.

Possible ontogenetic origins of the behaviour. Our analyses do not allow determining the ontogenetic origin of this unique social behaviour of rhythmic entrainment. However, it is likely that it emerged as a result of early sensorial and social (maternal) deprivation caused before the individuals moved to their current accredited institution (see Methods). The development of stereotypical movement is known to occur in similar conditions in other primates, including (“institutionalized”) children (see video link, https://www.youtube.com/watch?v=VGeWr8OFuEs) due to the lack of maternal contact during infancy. Given that stereotypical behaviours emerge spontaneously, this is could be also the case with this unique example of synced co-stereotypy.
Chimpanzees are known to imitate behaviours of zoo visitors, but these cases of imitation involved exogenous (i.e. human primed/prompted) non-rhythmic individual behaviour. A similar human-seeded learning scenario to explain a distinct case of endogenous rhythmic social behaviour would rely on a chain of unlikely events. First, zoo visitors or staff would have to perform a close replica of the reported social rhythmic behaviour (i.e. conga-line) in front of the chimpanzee enclosure. This would open some basic logistical questions. For example, subjects used virtually the complete extension of the outside enclosure to perform the behaviour but the area associated with the visitor windows (where imitation ought to have been learned) was much smaller (and this is also typically the case with enclosures’ “backstage” with staff-only access). Second, demonstration-time would have to be sufficient to assure accurate transmission of behaviour involving two individuals. In light of what has been successfully implemented with do-as-I-do imitation games between humans and apes, demonstrations typically require multiple exposures but have never, to our knowledge, involved the simultaneous training of two individuals. If possible, this would at least compound the necessary demonstration time and require a very sophisticated reward method to maintain the two subjects equality engaged in the task. Third, only two individuals would have to acquire the behaviour but none of their conspecifics with whom they share their enclosure. Forth, the two subjects would have to continue exhibiting the behaviour well after the human demonstrators had left the scene. Fifth, animal training programs ceased in the early 1980’s at the zoo. It seems that any activity with unknown. Because stereotypic behaviour in captive animals, including primates, can be associated with confinement and distress, it is conceivable that natural conditions imposing similar effects could have played a role in dance (and perhaps more generally, music) emergence.

For instance, paleo-climate change shifted food source availability and distribution, putatively driving physiological stress, intra- and intergroup competition, effects that would have been further exacerbated where ancestral hominins were constrained into pockets of remaining habitat or ecological refugia. These conditions could have perhaps caused confinement effects similar to those experienced in captivity. Similarly, if the adoption of a
cooperative breeding system\(^{48}\) took place along the human lineage, this could have driven individuals to live in “crowded” niches, with non-reproducing and/or post-reproducing individuals remaining in the groups.

These specific scenarios will remain speculative until similar behaviours are identified across great apes (and possible other primates), however, considering that endogenous social rhythmic entrainment is now observed in chimpanzees outside human dance, future hypotheses and models of dance evolution should take into account (in some form and extent) that rhythmic entrainment may have emerged as a stress-coping co-stereotypy under increasing ecologically- and/or socially-induced stress. Other human derived features, such as niche construction\(^{49}\) through cumulative culture\(^{50}\) could have intensified this “natural captivity” or “self-domestication” effect.

**Conclusion**

Evolutionary inferences about human dance based on chimpanzee rhythmic entrainment are limited and should be taken thoughtfully. It is critical to note, however, that our data and interpretations contrast radically with scenarios previously put forward for dance and music evolution\(^{51,52}\). Past scenarios have been typically inspired either in modern day human dance/musical expression or in communication systems in further related animal lineages, mostly because these were, at the time, the only living models available. Both (human, and non-primate animal) models misrepresent, however, what may have been the function and form of proto-dance among our hominin ancestors due cultural and biological distance, respectively. Somewhat paradoxically and anachronistically, virtually all dance evolution research has, thus far, tested humans or animals with modern 20\(^{th}\) and 21\(^{st}\) century music\(^{53}\).

The case of chimpanzee endogenous social rhythmic entrainment, together with new data-driven testable frameworks\(^{54}\), provides an impulse for the advance of the study of dance evolution based on real and concrete behaviours\(^{55}\), including in our closest living relatives. Critically, our findings highlight (i) the importance of the social cohesion hypothesis for dance evolution via bottom-up evolutionary mechanisms, (ii) the importance of the socio-ecological environment as selective trigger for the evolution of human dance and (iii) the importance of stress-coping and social consolation behaviours as precursors for the evolution of human dance.

**Data availability**

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

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**References**

1. Cook, P., Rouse, A., Wilson, M. & Reichmuth, C. A California Sea Lion (Zalophus californianus) Can Keep the Beat: Motor Entrainment to Rhythmic Auditory Stimuli in a Non Vocal Mimic. *Journal of Comparative Psychology* **127**, No Pagination Specified (2013).
2. Fitch, T. W. Rhythmic cognition in humans and animals: distinguishing meter and pulse perception. *Frontiers in systems neuroscience* **7**, 68 (2013).
3. Patel, A. D. The evolutionary biology of musical rhythm: was Darwin wrong? *PLoS biology* **12**, e1001821 (2014).
4. Patel, A. D., Iversen, J. R., Bregman, M. R. & Schulz, I. Experimental Evidence for Synchronization to a Musical Beat in a Nonhuman Animal. *Current biology* **CB 19**, 827–830 (2009).
5. Schachner, A., Brady, T. F., Pepperberg, I. M. & Hauser, M. D. Spontaneous Motor Entrainment to Music in Multiple Vocal Mimicking Species. *Current biology* **CB 19**, 831–836 (2009).
6. Ravignani, A. et al. The Evolution of Rhythmic Cognition: New Perspectives and Technologies in Comparative Research. In *Proceedings of the Annual Meeting of the Cognitive Science Society* (Vol. 35, No. 35) (2013).
7. Brown, S. The ‘musilanguage’ model of music evolution. In *The Origins of Music* (eds Wallin, N. & Brown, S.) 271–300 (MIT Press, 1999).
8. Laland, K., Wilkins, C. & Clayton, N. The evolution of dance. *Current Biology* **26**, R5–R9 (2016).
9. McDermott, J. The evolution of music. *Nature* **453**, 287–288 (2008).
10. Brown, S., Merker, B. & Wallin, N. An introduction to evolutionary musicology. In *The Origins of Music* (eds Wallin, N., Merker, B. & Brown, S.) 3–24 (MIT Press, 1999).
11. Ravignani, A. & Cook, P. F. The evolutionary biology of dance without frills. *Current Biology* **26**, R878–R879 (2016).
12. Ravignani, A. Interdisciplinary debate: Agree on definitions of synchrony. *Nature* **545**, 158–158 (2017).
13. Merker, B., Morley, I. & Zuidema, W. Five fundamental constraints on theories of the origins of music. *Phil Trans R Soc B* **370**, 20140095–20140095 (2015).
14. Gámez, J. et al. Predictive rhythmic tapping to isochronous and tempo changing metronomes in the nonhuman primate. *Ann N Y Acad Sci* **1423**, 396–414 (2018).
15. Large, E. W. & Gray, P. M. Spontaneous tempo and rhythmic entrainment in a bonobo (Pan paniscus). *Journal of comparative psychology* **129**, 317–328 (2015).
16. Bergman, T. J. Speech-like vocalized lip-smacking in geladas. *Current biology* **CB 23**, R268–R269 (2013).
17. Ghazanfar, A. A., Takahashi, D. Y., Mathur, N. & Fitch, T. W. Cineradiography of monkey lip-smacking reveals putative precursors of speech dynamics. *Current biology* **CB 22**, 1176–1182 (2012).
18. Lameira, A. R. et al. Speech-like rhythm in a voiced and voiceless orangutan call. *PLoS one* **10**, e116136 (2015).
19. Lameira, A. R. & Wich, S. Orangutan Long Call Degradation and Individuality Over Distance: A Playback Approach. *International Journal of Primatology* **29**, 615–625 (2008).
20. Arcadia, A., Robert, D. & Boesch, C. Buttress drumming by wild chimpanzees: Temporal patterning, phrase integration into loud calls, and preliminary evidence for individual distinctiveness. *Primates* **39**, 505–518 (1998).
21. Dufour, V., Poulin, N., Curie, C. & Sterck, E. H. Chimpanzee drumming: a spontaneous performance with characteristics of human musical drumming. *Scientific reports* **5**, 11320 (2015).
22. Fuhrmann, D., Ravignani, A., Sarah, M.-P. & Whiten, A. Synchrony and motor mimicking in chimpanzee observational learning. *Sci Rep* **4**, 505283 (2015).
23. Haminen, L. & Pastelli, M. Cowlog: open-source software for coding behaviors from digital video. *Behavior research methods* **41**, 472–476 (2009).
24. Team, R. R.: A language and environment for statistical computing (2013).
25. Lund, U., Agostinelli, C. & Agostinelli, M. Package ‘circlize’ (2017).
26. Pfaff, B. VAR, SVAR and SVEC models: Implementation within R package vars. *Journal of Statistical Software* (2008).
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Author contributions

Conceived study: A.R.L.; Conducted analyses: A.R.L., T.E., A.R.; Wrote the article: A.R.L., T.E., A.R.

Competing interests

The authors declare no competing interests.

Additional information

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