Inter-individual coordination in walking chimpanzees

Highlights

- Chimpanzees, walking close to conspecifics, synchronize their gait pattern

- This inter-limb entrainment was more pronounced in individuals of similar height

- Social factors seemed to not affect entrainment intensity

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In brief

People walking next to each other fall often unconsciously into the same rhythm. Schweinfurth et al. investigated this effect in our closest-living relative, the chimpanzee, and found that chimpanzees spontaneously synchronize their walking patterns, too.

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Inter-individual coordination in walking chimpanzees

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SUMMARY

Humans, like many other animals, live in groups and coordinate actions with others in social settings.[1] Such interpersonal coordination may emerge unconsciously and when the goal is not the coordination of movements, as when falling into the same rhythm when walking together.[2] Although one of our closest living relatives, the chimpanzee (*Pan troglodytes*), shows the ability to succeed in complex joint action tasks where coordination is the goal,[3] little is known about simpler forms of joint action. Here, we examine whether chimpanzees spontaneously synchronize their actions with conspecifics while walking together. We collected data on individual walking behavior of two groups of chimpanzees under semi-natural conditions. In addition, we assessed social relationships to investigate potential effects on the strength of coordination. When walking with a conspecific, individuals walked faster than when alone. The relative phase was symmetrically distributed around 0° with the highest frequencies around 0, indicating a tendency to coordinate actions. Further, coordination was stronger when walking with a partner compared with two individuals walking independently. Although the inter-limb entrainment was more pronounced between individuals of similar age as a proxy for height, it was not affected by the kinship or bonding status of the walkers or the behaviors they engaged in immediately after the walk. We conclude that chimpanzees adapt their individual behavior to temporally coordinate actions with others, which might provide a basis for engaging in other more complex forms of joint action. This spontaneous form of inter-individual coordination, often called entrainment, is thus shared with humans.

RESULTS AND DISCUSSION

Joint action can be defined as any form of social interaction, whereby two or more individuals coordinate their actions in space and time to bring about a change in the environment.[4] Sometimes, coordination is the goal of an interaction, for instance, when two or more people are dancing with each other. However, unintentional coordination also occurs in interactions where the goal is not the interpersonal coordination of movements, for instance, when two or more people are walking side-by-side.[5,6] This interpersonal coordination of movements is often called entrainment and relies on perception-action links that become coupled.[7,8] Furthermore, even when people are asked not to entrain their actions with others, they cannot stop themselves from entraining their actions.[9,10] Entrainment has also observed in social vocalizations, like signing in a chorus or in asocial situations, like head bobbing to a beat.[11]

Although studies on joint action in humans are increasing because they are considered a hallmark of human interactions, less is known about joint action in other animals.[12,13] In contrast to humans, chimpanzees (*Pan troglodytes*), for example, do not show the same preference for joint action, if a goal can be achieved individually.[14,15] Chimpanzees are particularly interesting as they are one of our closest living relatives[16] and a good model for our last common ancestor with other African great apes.[17] One experimental task that has been repeatedly used to investigate joint action is the loose-string task.[18,19] Here, pairs of chimpanzees need to align their actions in space and time by performing the same action, which is pulling a string together to bring food into reach. Based on several experimental studies under highly controlled conditions, it has been concluded that chimpanzees can learn to coordinate actions,[19] understand that a partner is needed,[20] and that they can inhibit their action until a partner joins them.[21] Further, chimpanzees in the wild adjust their calls to the calls of others and engage in joint pant-hoots.[22] Overall, however, they are less motivated to perform joint action than humans.[3,23]

Coordinated actions in chimpanzees

Given that most studies on chimpanzee coordination are based on carefully controlled laboratory experiments, inter-individual action coordination under more natural conditions has so far not been reported, although studies addressing such coordination would be beneficial to provide a more comprehensive understanding of non-human entrainment.[24] We investigated whether chimpanzees spontaneously coordinate their actions

Figure 1. Chimpanzees walking together
Two adult male chimpanzees walking behind each other.

in a semi-natural environment when coordination was neither planned nor the goal of an interaction, i.e., when they were walking next to each other. Chimpanzees, of both social groups that were studied, were observed to walk together (Figure 1), which included kin (15%) and non-kin, same-sex (77%) and opposite sex dyads, as well as dyads with an age difference ranging from 0 to 23 years. This broadly reflects their social structure of 18% kin and 86% same-sex dyads and a maximum age range of 0–29 years. When the chimpanzees walked together, a step by one walker was followed by the same respective foot of the other walker in 79% of the cases within less than ±0.5 s (note, this is a more informative measure than phase locking, which is commonly reported for human walking patterns,[2] due to the lower temporal resolution of our video recordings). To measure inter-individual coordination, we calculated phase relationship values, which is an established method (cf. van Ulzen et al.[5]). When the chimpanzees walked next to each other, the phase relationship values (Figure 2) were not uniformly distributed (Kolmogorov-Smirnov test: D = 0.59, n = 23, p = 0.017) and can be best described as a unimodal distribution (Hartigans' dip test: D = 0.06, p = 0.85) with a peak at 0°. These data follow a von Mises distribution (Watson's test: 0.028, n = 23, p > 0.10), suggesting a circular normal distribution. Hence, these data show that the chimpanzees respond to the movements of conspecifics with only short delays in between placing the same respective foot. In addition, the phase relationship data with a peak around zero is in accordance with in-phase interindividual coordination, rather than out of phase coordination around 180°.

## Coordinated actions only in social situations

Next, we compared the walking behavior between different conditions to investigate whether seemingly coordinated actions emerge just by chance, which was not the case. Chimpanzees walked faster, i.e., more steps per second, when walking with another chimpanzee compared with when walking alone and without visual contact between the walker and other group members (generalized linear mixed model [GLMM]: β = 0.20 ± 0.08, n = 23, p = 0.020; Figure 3). This might be the result of social facilitation, i.e., the influence of an individual on another by its sheer presence[25] or by different underlying goals of walking. Like chimpanzees, humans respond generally faster in joint compared with individual tasks by initiating actions earlier.[26] However, joint actions are not per se faster. Particularly fast-acting young chimpanzees in an individual finger-tapping task slowed down their actions when they had to coordinate actions with their slower mothers.[27] Adjusting the speed of actions provides further evidence that the chimpanzees adapt their

behavior toward others when walking with them. In addition, when the chimpanzees walked together, the phase relationship values were shorter and showed less variation, suggesting more coordination, compared with when individuals were walking independently (Fisher's test: F = 222.79, df = 84, n = 23, p < 0.001; Figure 4). Thus, only when they walk together, chimpanzees show inter-individual temporal coordination of their gait, which is not a pattern that emerges by chance.

These results add to the scarce literature on inter-individual motor entrainment in chimpanzees. For example, in a recent study on captive chimpanzees, two females were observed to engage in coordinated bipedalism.[28] In this study, haptic coupling played a crucial role, as the chimpanzees typically collected an object before their walk and maintained mutual contact throughout the joint action. In a further study, one of the four tested chimpanzees coordinated her finger taps on a touch screen monitor with those of her daughter.[29] Coordination only occurred when she had auditory information of her daughter, which is an example of auditory coupling. The chimpanzees in our study were close, but not in direct contact with each other. Thus, their entrainment cannot be explained by haptic coupling. Given that the individuals were within 5 m to each other, we think coupling was mainly visual but auditory information may have played a role as well. Taken together, these studies suggest that chimpanzees entrain their actions with others, using various modalities. Furthermore, a study on three Japanese macaques demonstrated that they can synchronize their actions when pressing a button[30] (but see Merker et al.[31]), and a study on one bonobo showed that she could coordinate drumming a tube drum with a human experimenter.[32] Hence, such coordinated movements might be common also in other primates. However, how widespread joint action based on entrainment is should be subject for future studies.

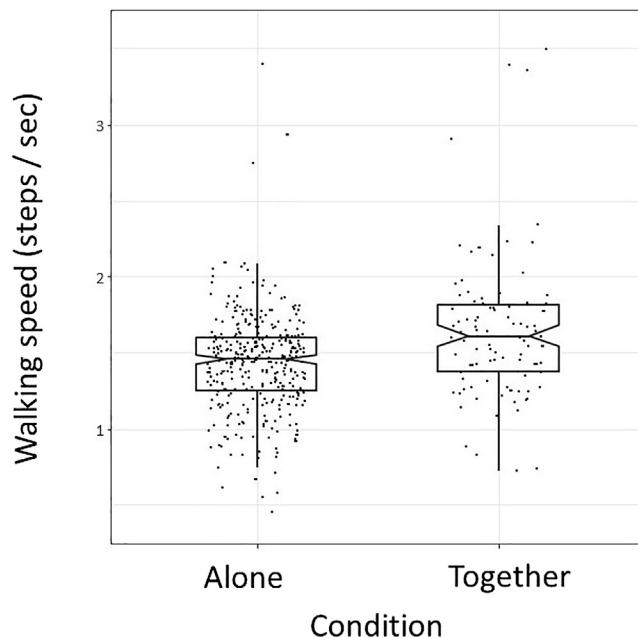## Coordination between chimpanzees in comparison to humans

It should be noted that when comparing the coordinated walking behavior of chimpanzees with joint walking patterns in humans (reviewed in Felsberg and Rhea[2]), the phase relationship histogram of chimpanzees shows a less clear peak. Two reasons could explain this result. Either entrainment is less pronounced in chimpanzees compared with humans or it was partially masked by increased noise during data collection. On one hand, low coordination values could reflect their tendency to be less in-phase (±0°) than humans or to avoid walking out of phase (±180°). Indeed, we found no evidence of walking anti-phase, and their tendency to coordinate around zero could reflect an avoidance of walking completely out of phase rather than a preference for walking in-phase. An avoidance of anti-phase coordination could explain the greater spread of the data in chimpanzees compared with humans. However, it is
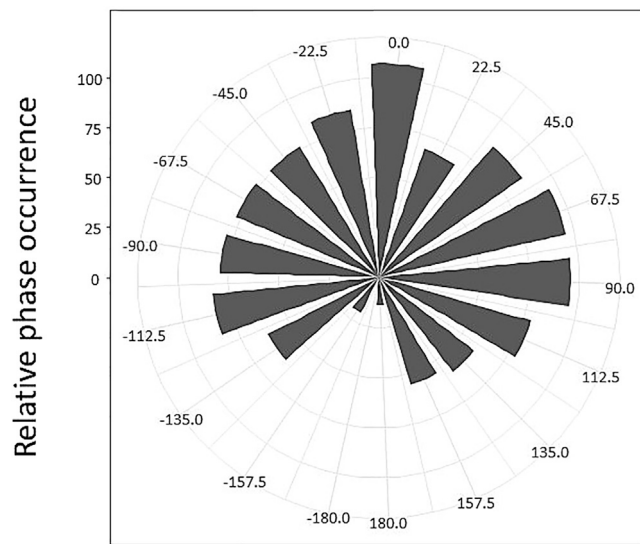
Figure 2. Circular histogram of the observed phase relationships between steps as a function of the required relative phase
Phase relationship for footfalls between chimpanzees walking close to each other.

Figure 3. Walking speed of chimpanzees when observed alone or with another chimpanzee
Chimpanzees walked faster (y axis) when walking with another chimpanzee compared with when walking alone. Shown is the median speed with the second and third quartile as box around. The notches indicate the 95% confidence interval around the median. Four outliers were removed for illustration purposes, but they were part of the analyses.

difficult to distinguish between those motivations in non-verbal individuals.

On the other hand, the data collection method differed in several aspects from studies on humans. First, although human participants are usually invited into the lab to walk on a treadmill, the chimpanzees were freely moving in their enclosure on an uneven ground with vegetation and in presence of potentially interfering group members, which is known to affect entrainment strength.[2] In addition, chimpanzees are quadrupedal and sometimes store food or items in their hands and feet while walking. Those factors likely impacted their gait patterns. Second, studies with humans usually make use of LED markers affixed to their participants and record their movements with high temporal resolution of 170 Hz,[6] which was not possible here with freely moving chimpanzees and possibly introduced a larger random error when computing the relative phase. Third, we opportunistically recorded their walking sequences, which were shorter than those usually recorded in humans, i.e., approximately 15 s compared with 60 s trials in human studies (e.g., Nessler and Gilliland[33]). This has left us with fewer iterations to detect entrainment effects, which emerge over time.[34] Fourth, the chimpanzees varied vastly in their size with some adolescent individuals being less than half the size of other chimpanzees in their group. Since the natural oscillation frequency is related to leg length, which affects entrainment in humans,[33] this affected coordination levels in our sample, too. Individuals with a greater age difference, which served as a proxy for height difference since the latter could not be assessed, tended to show longer phase relationships than those with smaller differences (linear mixed model [LMM]: $\beta = 1.75 \pm 0.98$, $\chi^2 = 3.45$, df = 1, n = 23, p = 0.06; Figure S1). In addition, the smaller their age difference, the less varied their phase relationships (Spearman's rank correlation: S = 136,537, n = 23, p = 0.021). Finally, only approximately 50% of the participants in human studies show

entrained actions when they are not instructed to do so.[35] Here, 35% of the chimpanzee dyads that walked together showed an average relative phase relationship of around 0° (±22.5°). All those factors hamper direct comparisons with human data.

Despite this noise, however, the phase relationship values for chimpanzees following each other showed a non-equal von Mises distribution with a peak around 0°, and the values were shorter than when they were walking independently. In fact, the noise might have led to an underestimation of the entrainment effects in our closest-living primate relative. Comparative analyses under similar conditions will be needed to directly compare entrainment levels between humans and chimpanzees.

Social factors affecting coordination
Although entrainment is an automatic and involuntary process, it has been argued to facilitate more complex forms of joint action, which require shared goals or joint intentionality. This is not only because entrainment can support predictions about what, where, and when the actions of others happen[36] but also because it increases social connectivity.[10] For example, friends show greater movement coordination during conversations than strangers.[37] This illustrates that entrainment is responsive to other more cognate processes, enabling joint action.[8] Chimpanzees form long-lasting bonds,[38] but we could not detect an effect of social bonds on entrainment (LMM: $\beta = 25.81 \pm 75.95$, $\chi^2 = 0.17$, df = 1, n = 23, p = 0.68; Spearman's rank correlation: S = 172,730, n = 23, p = 0.82; Figure S2). This absence might be
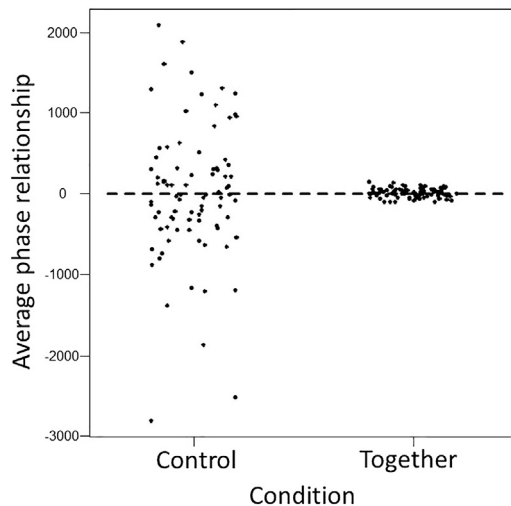
Figure 4. Average phase relationship between two individuals placing the respective feet when walking with each other compared with when independent walking patterns were matched

The average phase relationship values between steps (y axis) were shorter when walking close to another chimpanzee ("together") compared with when individual walking patterns were combined ("control"). The dotted line indicates zero.

See also Figures S1–S4.

explained by the effect of affiliation on entrainment being more short term. For instance, if individuals exchanged food or other affiliative behaviors shortly before the walk, they might be more likely to coordinate their steps, which could overwrite the effects of longer lasting social bonds. Future studies could investigate such short-term effects by sampling affiliative behaviors immediately before individuals start walking together.

Similar to socially bonded partners, relatives usually support each other unconditionally and to a larger extend than unrelated individuals (e.g., Silk et al.[39]). To receive comparable support from non-relatives, it might be necessary to invest into relationships with unrelated individuals.[40–42] Still, kinship had no effect on coordination levels (LMM: $\beta = -12.20 \pm 19.09$, $\chi^2 = 0.46$, df = 1, n = 23, p = 0.50; Fisher's test: F = 0.45, df = 12, n = 23, p = 0.12; Figure S3).

Given that none of the here investigated social factors seemed to influence coordination levels in chimpanzees, their tightly coupled inter-individual walking patterns might be based on sensorimotor co-timing. To which degree human coordination is also driven by non-social factors is not well understood, but studies with strangers (cf. Latif et al.[37]) suggest that coordination cannot solely be explained by social factors.

Coordination affecting affiliative behaviors
Entrainment levels can also affect prosocial emotions or actions.[43] For example, people who engaged in joint action, e.g., by swinging a pendulum or rocking in a chair in the same rhythm, report greater social connection, like more positive feelings about their partner and a greater sense of team spirit (reviewed in Marsh et al.[10]). This effect emerges early in ontogeny as 14-month-old infants preferentially help those

who coordinate their actions with them.[44] Therefore, we predicted that entrained movements could be positively linked with affiliative behaviors, happening immediately after walking together. However, whether the chimpanzees ended in such a positive compared with neutral interaction (like autogrooming or feeding) was not linked with their phase relationship (LMM: $\beta = 5.90 \pm 13.98$, $\chi^2 = 0.20$, df = 1, n = 23, p = 0.66; Fisher's test: F = 1.30, df = 70, n = 23, p = 0.48; Figure S4). This suggests that entrained gait patterns seem to not impact subsequent affiliation or prosociality in chimpanzees.

Conclusions
Chimpanzees show different forms of joint action.[3] So far, the focus of research on joint action in chimpanzees has been on strategic planning, like in the loose-string task, or complex coordination in economic games, like in the equity test,[45] ultimatum game,[46] or stag-hare game,[47] with mixed findings.[48] However, little is known about simpler forms of joint action, such as a tendency to fall into inter-individual coordination, which might be explained by entrainment. Entrainment has been described as a potential enhancing factor for more sophisticated forms of joint action, although it is not sufficient to produce them.[8] Understanding which mechanisms humans share with other species can help us understand the evolutionary origins of more sophisticated forms of joint action. This study provides evidence that chimpanzees temporally entrain their body movements to the movements of their conspecifics. Hence, chimpanzees share this basic mechanism with humans. Consequently, differences in joint action, of which some are supported by entrainment, might be due to other underlying mechanisms, like joint action goals. Although we observed inter-individual coordination in a social context, it seemed unaffected by social factors. Coordination was neither linked with long-term bonding nor kinship. Furthermore, coordination levels did not result in increased affiliative behavior, like grooming, between individuals immediately following their joint walk. By studying different processes that work in concert to enable joint action, we will be in better position to understand how joint action can emerge and be maintained. It will also enable us to take a more holistic approach to this topic not exclusively focused on strategic coordination and the putatively high-level cognitive processes that support it.

STAR★METHODS

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data	This paper	https://doi.org/10.17630/e39f1c62-b7a2-4539-bcae-baf7c538663b
Example video	This paper	Video S1
Experimental models: Organisms/strains		
Chimpanzees (*Pan troglodytes* spec.)	Chimfunshi Wildlife Orphanage Trust, Zambia	N/A
Software and algorithms		
R	R Foundation	https://www.r-project.org/
BORIS	Olivier Friard and Marco Gamba	https://www.boris.unito.it/
Other		
Canon Legria HF R806	Canon	N/A

RESOURCE AVAILABILITY

Lead contact
Further information and requests should be directed to the lead contact Manon Schweinfurth (ms397@st-andrews.ac.uk).

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

Data and code availability
An example video can be found in Video S1. The research data underpinning this publication can be accessed at https://doi.org/10.17630/e39f1c62-b7a2-4539-bcae-baf7c538663b.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subjects and study site
This study was conducted in 2019 at the Chimfunshi Wildlife Orphanage Trust, which is an open-air chimpanzee sanctuary located in North-Western Zambia. In Chimfunshi, the chimpanzees live in social groups comprised of sanctuary-born and wild-born individuals, which were orphanaged because of illegal bush meat hunt on their mothers. In this study, we worked with two groups (group 3 and 4), comprised of 11 individuals (seven adults [4 females and 3 males] and four juveniles [2/2], of which five were wild born) and 13 individuals (eight adults [3/7] and three juveniles [1/2], of which nine were wild born), respectively. Group 3 lives in an enclosure of 47 acres and group 4 in 62 acres. During feeding times (two hours a day), chimpanzees are called into indoor handling facilities with several rooms. There, they are provided with *nshima* balls (maze flour cooked with water) and local seasonal fruits and vegetables. Outside the feeding time, the individuals can freely range in their enclosures. The enclosures resemble the natural habitat of chimpanzees and thus allow naturalistic observations in captivity.[49] More information on the two groups can be found in Table S1.

Ethical note
All procedures were non-invasive. We adhered to the legal requirements of the Republic of Zambia (Prevention of Cruelty to Animals Act) and the United Kingdom (Animals Scientific Procedures Act 1986). In addition, our experimental design and treatment of animals followed the guidelines of the 'Association for the Study of Animal Behaviour', the 'Pan African Sanctuary Alliance guidelines' and the 'Code of Best Practices for Field Primatology' by the International Primate Society. Our study was approved by the ethics committee of the University of St Andrews (School of Psychology and Neuroscience Ethics Committee) and the host sanctuary (Chimfunshi Research Advisory Board). During our study, the chimpanzees were never food or water deprived. We avoided any exaggerated or swift movements in their presence and kept a safety distance of more than one meter to their fence to not infer with the chimpanzees for this observational study.

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METHOD DETAILS

Over three months and for two hours each day, we observed the whole group. On an all-occurrence basis, we video recorded (Canon Legria HF R806, 25 frames per second) individuals whenever two individuals walked within five meters side-by-side (76 steps) or behind (2269 steps) each other ('walking together' condition, 102 videos with an average of 15.64 steps ± a standard deviation of 13.46 steps, see also Video S1). Five meters was chosen as this is a distance in which individuals interact and which is commonly used in nearest neighbour assessments (see for instance Machanda et al.[50]). The distance was assessed visually with the help of the fence poles. For each video, we noted the identity of the chimpanzees and the timing of placing their feet on the ground. We used their feet as there was less variability in their walking patterns when looking at their feet than hands. In addition, the timing of placing a foot was easier to detect than their hands. We then calculated the walking speed for the two walkers (i.e., steps divided by time) and the delay between both walking in phase (i.e., the time in between placing the same respective foot). Additionally, we noted whether the walkers ended in a neutral state (e.g., grooming themselves, in contact with others, or feeding) or a positive state (grooming each other, sitting in contact with each other, playing with each other, or having sex).

We also recorded individuals when they were walking alone with no other chimpanzees walking within five meters to them and when there was no visual contact between the focal individual and other chimpanzees ('walking alone' condition, 353 videos, 24.74 ± 13.47 steps). Again, we noted the identity of the chimpanzee and the timing of placing their feet on the ground. We then calculated the walking speed (i.e., steps divided by time). To establish a control condition for the 'walking together' condition, we combined individual walking patterns of the same individuals that we observed in the social condition, where we had such data ('control' condition, 85 videos) and calculated the delay between both walking in phase.

In addition, we conducted proximity scans once a week for nine weeks as a proxy for social bonds. From 9:00 until 11:20, which is shortly before feeding, and from 13:40 until 15:40, which is shortly after feeding, we recorded who was within a five meters range to each group member every ten minutes. Based on this, we calculated the sum of individual A interacting with individual B, divided by the sum of all interactions of A. The proximity scores, used for the analyses, were the average of all observations. The data was complemented with kinship and age information, provided by the sanctuary, based on observations and genetic analyses (Table S1).

QUANTIFICATION AND STATISTICAL ANALYSIS

Data coding
We only used videos where we could observe the footfalls of individuals clearly for more than five consecutive steps and coded them using Boris 7.10.2 (https://www.boris.unito.it/). A second coder scored 10% of the videos, which were randomly picked from all conditions, to assess inter-observer reliability. Their ratings of the walking behavior were highly correlated ($F_{63}= 6.32$, $p < 0.0001$, Cohen's $\kappa = 0.73$).

Phase relationship
For each step of the two walkers, we used the delay (D) in between placing the same foot, e.g., left foot of individual A and closest left foot of individual B at a given time (t_1). Individual A was the spatial leader in conditions where chimpanzees walked together. For the control condition, the individual of which we could code the first step was determined to be A. This delay was corrected for the walking speed of the two walkers by dividing this value by the time in between placing this foot and the previous same foot of both walkers (t_0), which was divided by two to account for the two walkers. The value was multiplied by 360° to obtain the phase relationship between steps (see equation below).

$$Phase\ relationship: \ \varphi(t) \ = \ \frac{\left(D_{A(t1)} - D_{B(t1)}\right)}{\left(D_{A(t1-t0)} - D_{B(t1-t0)}\right)/2} \times 360°$$

Statistical analyses
All graphs and analyses were conducted in R 3.6.0 with RStudio and the 'circular,[51]' 'diptest,[52]' 'ggplot2,[53]' 'irr,[54]' 'lme4,[55]' and 'MASS[56]' packages.

To test whether the distribution of the phase relationship values in the 'walking together' condition follows an equal distribution, we used a Kolmogorov Smirnoff test. We further tested whether the distribution showed a multimodal distribution, using Hartigans' Dip test for unimodality. Finally, we tested whether the data followed a circular normal distribution, i.e. von Mises distribution,[57] using Watson's goodness of fit test. To compare the variance between the 'walking together' and 'control condition' data, we used Fisher's test to compare average phase relationships per walking sequence.

To investigate underlying mechanisms of the entrainment, we fitted linear mixed models (LMM) or generalized linear mixed models (GLMM) and checked the model fit with the help of Q-Q plots or with overdispersion tests. First, we investigated whether the speed of individuals was different between walking alone compared to when walking with another individual. For this, we included walking speed as response variable and condition (alone vs. together) as factor with identity as random

effect, using a GLMM. We further tested whether the phase relationship was influenced by several factors. Here, we calculated the average phase relationship per walking sequence and included the dyad's proximity score and age difference (as a proxy for height since no weight or size measurements could be taken from the animals) as covariates, kinship as factor (non-kin vs. kin, i.e., parent-offspring and siblings) and the identity of both walkers and their dyad number as random effects. Furthermore, we conducted a separate model with end state (neutral vs. positive) as factor, using the same model structure as previously described. In addition, we compared the variance for the kinship and end state data, using Fisher's test, and correlated the model's residuals with the proximity and age difference values, using Spearman's test.