




OPEN The work to swing limbs in humans versus chimpanzees and its relation to the metabolic cost of walking

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Compared to their closest ape relatives, humans walk bipedally with lower metabolic cost (C) and less mechanical work to move their body center of mass (external mechanical work, W_{EXT}). However, differences in W_{EXT} are not large enough to explain the observed lower C : humans may also do less work to move limbs relative to their body center of mass (internal kinetic mechanical work, $W_{INT,k}$). From published data, we estimated differences in $W_{INT,k}$, total mechanical work (W_{TOT}), and efficiency between humans and chimpanzees walking bipedally. Estimated $W_{INT,k}$ is ~60% lower in humans due to changes in limb mass distribution, lower stride frequency and duty factor. When summing $W_{INT,k}$ to W_{EXT} , between-species differences in efficiency are smaller than those in C ; variations in W_{TOT} correlate with between-species, but not within-species, differences in C . These results partially support the hypothesis that the low cost of human walking is due to the concerted low $W_{INT,k}$ and W_{EXT} .

List of symbols

a	Proximal distance of the lower limb center of mass as a fraction of limb length
b	Upper limb length as a fraction of lower limb length
C	Metabolic cost
d	Duty factor
EqO_2	Energy equivalent of oxygen
Fr	Froude number
g	Gravity acceleration
m	Body mass
m^L	mass of the lower limb as fraction of body mass
m^U	mass of the upper limb as fraction of body mass
q^I	Inertial factor
R	Average length of the four limbs
R_L	Lower limb (hindlimb) length
R_U	Upper limb (forelimb) length
SF	Stride frequency
v	Average progression speed
VO_{2rest}	Oxygen uptake at rest
VO_{2ss}	Oxygen uptake at steady state
W_{EXT}	External mechanical work
$W_{INT,f}$	Internal frictional mechanical work
$W_{INT,k}$	Internal kinetic mechanical work
W_{TOT}	Total mechanical work
β	Damping coefficient
β_L	Sum of the damping coefficients for the lower limb (hindlimb)
β_U	Sum of the damping coefficients for the upper limb (forelimb)
γ	Limb radius of gyration as a fraction of limb length
γ_L	Radius of gyration of the lower limb (hindlimb) as a fraction of limb length
γ_U	Radius of gyration of the upper limb (forelimb) as a fraction of limb length

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Humans walk with lower metabolic energy demands than their closest ape relatives^{1–3}. This may have enabled them to economically forage in environments with low food density and has been pivotal for their expansion and prosperity^{1,4,5}. To understand how such economical locomotion is achieved, researchers have compared humans to chimpanzees, since they are phylogenetically close to humans and facultative bipeds when free-ranging^{6–10}; humans expend less than half metabolic energy than chimpanzees during bipedal locomotion, and such a difference correlates with active limb muscle volume estimated through inverse dynamics^{1–3,5,11}. Coherently, humans walk with more favourable pendular mechanics of their body center of mass and do ~50% less work to lift and accelerate it compared with chimpanzees (external mechanical work, W_{EXT})^{6,12}. Differences in body center of mass mechanics may be driven by anatomical factors, such as longer hindlimbs in humans¹³, narrower pelvis with a shorter and more dorsally projecting ischium¹⁴, greater bicondylar valgus knee angle^{6,15}, a more adducted hallux and stiffer midfoot^{16,17}, the latter aspects favoring the ability to walk with a heel-to-toe rolling pattern¹⁸ and push-off mechanics¹⁷. Recently, O'Neill and colleagues¹⁹ have also shown that the summed dimensionless joint work at hip, knee, and ankle joints is ~25% lower in humans than chimpanzees, and ~45% lower when elastic energy storage is accounted for.

However, do the observed differences in walking mechanics fully explain reductions in metabolic demands? In humans, W_{EXT} is 50–70% of total mechanical work (W_{TOT})²⁰ so a 50% lower W_{EXT} without changes in efficiency, would lower metabolic demands by no more than 35%. W_{TOT} also includes the work done to swing limbs with respect to the body center of mass (internal kinetic mechanical work, $W_{INT,k}$)^{21,22}, which may be sensibly lower in humans than in chimpanzees based on several observations. Humans have a two-fold lower moment of inertia of the upper limb^{23,24}, which lowers the work required to swing it^{19,25}. Moreover, Human lower limb is longer than chimpanzees' hindlimb^{23,24,26}. This increases the moment of inertia but decreases the number of acceleration-deceleration cycles for a given walking distance²⁷; at matched speeds, humans walk with lower stride frequencies than chimpanzees^{2,28,29}. Finally, humans may also walk with a lower duty factor^{2,28}—the fraction of the stride period in which a limb contacts the ground—which reduces limb acceleration during swing. Although well-characterized in humans, $W_{INT,k}$ is unknown for chimpanzees walking bipedally. Knowing it would allow a comparison between the two species and an assessment of differences in W_{TOT} and locomotor efficiency, the ratio of mechanical work to metabolic cost²¹. In the present work, we analyze literature data on bipedal walking in the two species and assess the following hypotheses: (i) $W_{INT,k}$ is substantially lower in humans than in chimpanzees; (ii) once $W_{INT,k}$ is accounted for, interspecies differences in W_{TOT} are approximately proportional to differences in metabolic demands.

Materials and methods

Data sources

This work draws on published data on bipedal walking for chimpanzees^{2,6} and humans²⁹. All such data are available in text, tables, figures, and supplementary materials of the cited papers except for duty factor data from Pavei et al.²⁹, which were shared by the authors. The following sections show how mechanical and metabolic variables were estimated from them. Table 1 summarizes the demographic and biometric characteristics of the study participants.

Internal kinetic mechanical work

Experimental measurements of $W_{INT,k}$ are unavailable for chimpanzees. However, in legged animals, $W_{INT,k}$ ($J\ kg^{-1}\ m^{-1}$) can be modeled as²⁸:

$$W_{INT,k} = SFv \left(1 + \left(\frac{d}{1-d} \right)^2 \right) q \quad (1)$$

where SF is the stride frequency (Hz), v is the average progression speed ($m\ s^{-1}$), d is the duty factor, and q is a dimensionless term that depends on the inertial properties of the limbs:

$$q = \frac{\pi^2}{4} [(a^2 + \gamma^2)(m'_L + b^2 m'_U)] \quad (2)$$

Source	Species	N	Sex	Age (years)		Body mass (kg)		Lower limb or hindlimb length (m)	
				Mean	SD	Mean	SD	Mean	SD
Pontzer et al. ²	Chimpanzees	5	F: 3 M: 2	19	11	59.9	19.5	0.46	0.05
Demes et al. ⁶	Chimpanzees	3	Not specified	6	0	28.7	6.4	0.38	0.03
Pavei et al. ²⁹	Humans	13	F: 7 M: 6	23	3	62.4	10.0	0.90	0.03

Table 1. Demographic and biometric characteristics of the study participants. For Demes et al.⁶, no information could be retrieved about sex.

where a and γ are the average proximal distance and gyration radius of the lower limb center of mass as a fraction of limb length, b is the upper limb length as a fraction of the lower one, and m'_L and m'_U are the masses as a fraction of body mass of the lower and upper limbs, respectively²⁸. This equation neglects differences in relative gyration radius between upper and lower limbs, which may be inappropriate when comparing $\dot{W}_{INT,k}$ between species since the proportional mass distribution between fore- and hindlimbs differs between humans and chimpanzees^{24,26,30,31}. A more general version of Eqs. (1) and (2) can be written from the original formulation by Minetti and Saibene³²:

$$\dot{W}_{INT,k} = SFv^2 \frac{\pi^2}{2} [a^2(m_L + b^2 m_U) + (m_L \gamma_L^2 + m_U b^2 \gamma_U^2)] \quad (3)$$

where $\dot{W}_{INT,k}$ is the mechanical internal power, and γ_L and γ_U are the gyration radii of the lower and upper limbs as a fraction of the respective limb length. To account for the duty factor, v^2 can be written as²⁸:

$$v^2 = \frac{1}{2} v_{ST}^2 + \frac{1}{2} v_{SW}^2 \quad (4)$$

where v_{ST} is the progression speed term, and v_{SW} is the term for the limb speed relative to the body center of mass. The relation between v_{SW} and the duty factor (d) is given by:

$$v_{SW} = v_{ST} \left(\frac{d}{1-d} \right) \quad (5)$$

Combining (4) and (5) yields:

$$v^2 = \frac{1}{2} v_{ST}^2 \left(1 + \left(\frac{d}{1-d} \right)^2 \right) \quad (6)$$

Therefore, $\dot{W}_{INT,k}$ is:

$$\dot{W}_{INT,k} = SFv_{ST}^2 \left(1 + \left(\frac{d}{1-d} \right)^2 \right) \frac{\pi^2}{4} [a^2(m_L + b^2 m_U) + (m_L \gamma_L^2 + m_U b^2 \gamma_U^2)] \quad (7)$$

Defining m'_L and m'_U as the fractional masses of the upper and lower limbs, and m as the total body mass:

$$\dot{W}_{INT,k} = mSFv_{ST}^2 \left(1 + \left(\frac{d}{1-d} \right)^2 \right) \frac{\pi^2}{4} [a^2(m'_L + b^2 m'_U) + (m'_L \gamma_L^2 + m'_U b^2 \gamma_U^2)] \quad (8)$$

Converting from mechanical power to the mechanical work performed to move a unit body mass per unit distance ($J \text{ kg}^{-1} \text{ m}^{-1}$):

$$W_{INT,k} = SFv_{ST} \left(1 + \left(\frac{d}{1-d} \right)^2 \right) \frac{\pi^2}{4} [a^2(m'_L + b^2 m'_U) + (m'_L \gamma_L^2 + m'_U b^2 \gamma_U^2)] \quad (9)$$

This equation only differs from the equation presented in the work of Minetti²⁸ in that it does not assume equal relative gyration radii for the upper and lower limbs. The term q' can be defined here as:

$$q' = \frac{\pi^2}{4} [a^2(m'_L + b^2 m'_U) + (m'_L \gamma_L^2 + m'_U b^2 \gamma_U^2)] \quad (10)$$

For which q is a special case when a unique radius of gyration relative to limb length (γ) is assumed for the upper and lower limbs ($\gamma_L = \gamma_U = \gamma$). Hence:

$$W_{INT,k} = SFv_{ST} \left(1 + \left(\frac{d}{1-d} \right)^2 \right) q' \quad (11)$$

This allowed estimating $W_{INT,k}$ for chimpanzees based on spatiotemporal data from Pontzer et al.²; for humans, $W_{INT,k}$ values were taken from Pavei et al.²⁹. This model assumes extended limbs but can be expanded to account for the bent-hip, bent-knee features of chimpanzees walking; the validity of such mechanical work estimates is discussed in Supplementary Material S1.

In addition to $W_{INT,k}$, work is done to overcome joint frictions during locomotion (*internal frictional mechanical work*, $W_{INT,f}$, $J \text{ kg}^{-1} \text{ m}^{-1}$)³³; this term is not estimated here for chimpanzees because experimental data on limb damping are lacking (Supplementary Material S2).

External mechanical work and total mechanical work

For humans, external mechanical work (W_{EXT}) increases with walking speed^{12,20,29}; however, for chimpanzees, such a relationship is less clear. Here W_{EXT} data for chimpanzees walking bipedally were taken from Demes et al.⁶ and fitted with zero, first- and second-order mixed effect models in the forms:

$$W_{EXT} = \beta_0 + b(1|participant) + \epsilon \quad (12)$$

$$W_{EXT} = \beta_0 + \beta_1 speed + b(1|participant) + \epsilon \tag{13}$$

$$W_{EXT} = \beta_0 + \beta_1 speed + \beta_2 speed^2 + b(1|participant) + \epsilon \tag{14}$$

where β and b are the fixed and random effect coefficients, respectively. The Akaike Information Criterion (AIC) was calculated, and the model with the lowest AIC was chosen. A zero-order model had the lowest AIC (Supplementary Material S3), so all the analyses in the present work used a speed-independent value of $0.55 \pm 0.18 \text{ J kg}^{-1} \text{ m}^{-1}$, equal to the mean W_{EXT} reported by Demes and colleagues⁶. All these analyses were done with R 3.6.2, R Studio 1.2, and lme4^{34–36}. W_{TOT} was then calculated as the sum of $W_{INT,k}$ and W_{EXT} , and its standard deviation as³⁷:

$$SD_{W_{TOT}} = \sqrt{SD_{W_{INT,k}}^2 + SD_{W_{EXT}}^2} \tag{15}$$

where $SD_{W_{INT,k}}$ and $SD_{W_{EXT}}$ are the standard deviations for $W_{INT,k}$ and W_{EXT} , respectively. For humans, experimental values for $W_{INT,k}$, W_{EXT} and W_{TOT} were taken from Pavei et al.²⁹.

Stride frequency and duty factor

For each species, stride frequency and duty factor values from Pavei et al.²⁹ and Pontzer et al.² were regressed over speed (Fig. 1). Then, percent variations were calculated from regression equations at the minimum (0.45 m s^{-1}) and maximum (1.67 m s^{-1}) common speeds between the two datasets and reported in Table 2. The uncertainties for SF and d were quantified by their standard deviations SD_{SF} and SD_d , and propagated as:

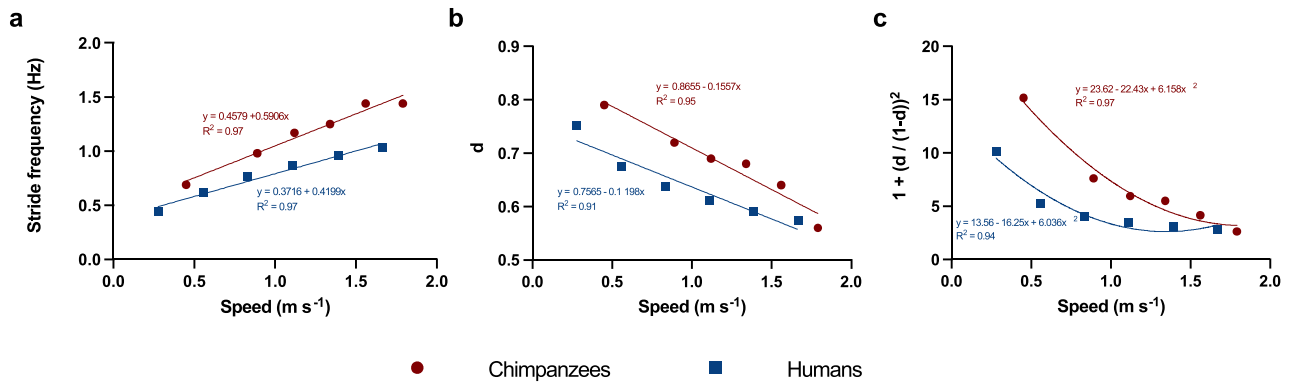


Figure 1. Spatiotemporal parameters. Stride frequency, duty factor (d) and the term $1 + (d/(1-d))^2$ from Eq. (11) are plotted for chimpanzees (red circles; data from Pontzer et al.²) and humans (blue squares; data from Pavei et al.²⁹). Species-specific linear and polynomial regression equations are shown, together with their coefficient of determination (R^2).

Parameter	Description	Chimpanzees	Humans	% difference
Inertial parameters				
a	Proximal distance of the lower limb center of mass as a fraction of lower limb length	0.336	0.280	– 17%
b	Upper limb length as a fraction of lower limb length	1.032	0.585	– 43%
m'_U	Upper limb mass as a fraction of body mass	0.084	0.047	– 44%
m'_L	Lower limb mass as a fraction of body mass	0.122	0.203	+ 67%
γ_U	Radius of gyration of the upper limb as a fraction of limb length	0.273	0.281	+ 3%
γ_L	Radius of gyration of the lower limb as a fraction of limb length	0.268	0.259	– 3%
q'	Inertial factor, given by $\frac{\pi^2}{4} [a^2(m'_L + b^2 m'_U) + (m'_L \gamma_L^2 + m'_U b^2 \gamma_U^2)]$	0.096	0.081	– 16%
Spatiotemporal parameters				
SF	Stride frequency (Hz)	[0.72; 1.44]	[0.56; 1.07]	[– 26%; – 22%]
d	Duty factor	[0.61; 0.80]	[0.56; 0.70]	[– 13%; – 8%]
$1 + \left(\frac{d}{1-d}\right)^2$	Function relating duty factor to $W_{INT,k}$ in Eq. (11)	[3.34; 14.77]	[3.26; 7.47]	[– 49%; – 2%]

Table 2. Determinants of $W_{INT,k}$. Human parameters were calculated from De Leva et al.²³ and Pavei et al.²⁹, mean of females and males. Parameters for chimpanzees were calculated from Druelle et al.³⁹ and Pontzer et al.², mean of females and males. For spatiotemporal parameters, brackets report the minimum and maximum values and percent variations in the common speed range ($0.45\text{--}1.67 \text{ m s}^{-1}$). % difference is calculated with respect to chimpanzee values.

$$SD_{W_{INT,k}} = \sqrt{\left(\frac{\partial W_{INT,k}}{\partial SF} \cdot SD_{SF}\right)^2 + \left(\frac{\partial W_{INT,k}}{\partial d} \cdot SD_d\right)^2} \quad (16)$$

to estimate how they impacted $SD_{W_{INT,k}}$ ³⁷. Of note, duty factor values were taken from Pontzer et al.², but O’Neill and colleagues³⁸ reported similar duty factors between three chimpanzees and three speed-matched humans. Despite this, duty factor values from the former study were chosen due to the larger number of chimpanzee participants and a wider range of walking speeds. In instances of smaller differences in duty factor, the resulting differences in $W_{INT,k}$ would be smaller but still be present, as indicated by error propagation and Table 2.

Metabolic cost and efficiency

To calculate efficiency, metabolic demands must be expressed in the same units as mechanical ones. Pontzer et al.² measured the oxygen uptake of five chimpanzees walking bipedally on a treadmill at various speeds. From these data, metabolic cost C ($J\ kg^{-1}\ m^{-1}$) can be calculated as^{40,41}:

$$C = \frac{(\dot{V}O_{2ss} - \dot{V}O_{2rest})EqO_2}{vm} \quad (17)$$

where VO_{2ss} and VO_{2rest} are the oxygen uptake during steady-state locomotion and at rest, respectively, m is the body mass (kg), and EqO_2 is the number of joules released during the combustion of one milliliter of oxygen. EqO_2 spans from 19.62 to 21.13 $J\ mL O_2^{-1}$ ⁴², and here a mean value of 20.9 J per $mL O_2$ is assumed. Efficiency is $W_{TOT} C^{-121}$; therefore, its standard deviation is given by³⁷:

$$SD_{efficiency} = \sqrt{\frac{W_{TOT}^2 SD_C^2 + SD_{W_{TOT}}^2 C^2}{C^4}} \quad (18)$$

where SD_C is the sample standard deviation for C . For humans, Pavei and colleagues²⁹ provide experimental measurements of C and efficiency. Each outcome variable was regressed over speed; due to the small sample size and the unsuitability of null hypothesis testing for such a study design, only regression parameters were reported together with their coefficient of determination (R^2).

Results

Compared with chimpanzees, humans have lower stride frequency and duty factor at all speeds, and a lower q' (Fig. 1, Table 2), leading to lower $W_{INT,k}$ (Fig. 2). In the common speed range 1.1–1.4 $m\ s^{-1}$, W_{EXT} ranges from 0.46 to 0.55 $J\ kg^{-1}\ m^{-1}$ for humans and averages 0.55 $J\ kg^{-1}\ m^{-1}$ for chimpanzees. Because of concomitantly decreased $W_{INT,k}$ and W_{EXT} , humans walk with less W_{TOT} than chimpanzees (Fig. 2, Supplementary Fig. S4). As values of C from humans are proportionally lower than those of chimpanzees at all speeds, between-species differences in efficiency are smaller than differences in either C or W_{TOT} (Fig. 2, Supplementary Fig. S4).

Discussion

In this paper, we provide evidence that humans walk bipedally with less mechanical internal work than chimpanzees. Total mechanical work is also lower in humans than in chimpanzees, making between-species differences in efficiency smaller than those in metabolic cost.

Mechanical work

At a given speed, $W_{INT,k}$ is proportional to three terms: stride frequency, a monotonous function of duty factor, and an ‘inertial term’ that lumps relative limb lengths and masses distribution²⁸ (Eq. 1). Such a model is coherent with stereophotogrammetric calculations of $W_{INT,k}$ ^{22,44}, and explains the mechanisms driving changes in $W_{INT,k}$ between and within species^{28,29,45}; however, it assumes equal relative gyration radii and center of mass position for all limbs. As limb mass distribution differs between chimpanzees and humans, we generalized such model to avoid these assumptions (Eqs. 10 and 11). The model also assumes fully extended limbs, but Supplementary Material S1 and Fig. 3 show that limb flexion would not relevantly alter calculations of mechanical work and efficiency. In the range of speeds between 0.45 and 1.67 $m\ s^{-1}$, humans walk with a lower stride frequency^{2,29}, contributing to a 22–25% reduction in estimated $W_{INT,k}$ (Table 2, Fig. 1); humans also have a lower duty factor at low speeds (which further reduces $W_{INT,k}$ by up to 49%), but this difference diminishes at higher speeds (Table 2, Supplementary Fig. S4). Even if the human upper limb has a greater relative gyration radius than chimpanzees’ forelimb, this is compensated by its lower fractional mass and length (Table 2)^{23,24}; altogether, this reduces q' , and hence $W_{INT,k}$ by an additional 16%. As a result, humans have a ~60% lower $W_{INT,k}$ than chimpanzees. These different strategies may reflect distinct optimization goals in the two species: a higher duty factor and stride frequency may optimize safety and stability in chimpanzees, while lowering them curbs the mechanical demands of walking in humans; greater distal masses in the upper limbs favor climbing and brachiation, while shifting them proximally and to the lower limbs reduces the cost of walking⁴⁶.

Besides $W_{INT,k}$, work is done to overcome joint friction during locomotion ($W_{INT,f}$)³³. Generalizing its formula, $W_{INT,f}$ is proportional to $\beta_U/R_U^2 + \beta_L/R_L^2$, where β_U , β_L , R_U , R_L are the damping coefficients ($N\ m\ s\ rad^{-1}$) and length (m) of the upper and lower limbs, respectively (Supplementary Material S2). If human damping coefficients β_U and β_L are taken from Minetti et al.³³ and the same are assumed for chimpanzees, humans would do less $W_{INT,f}$ because of the concomitantly increased R_U and R_L . However, this assumption is challenged by the interspecies differences in soft tissue distribution and anatomy of the proximal limb joints⁴⁷, potentially causing

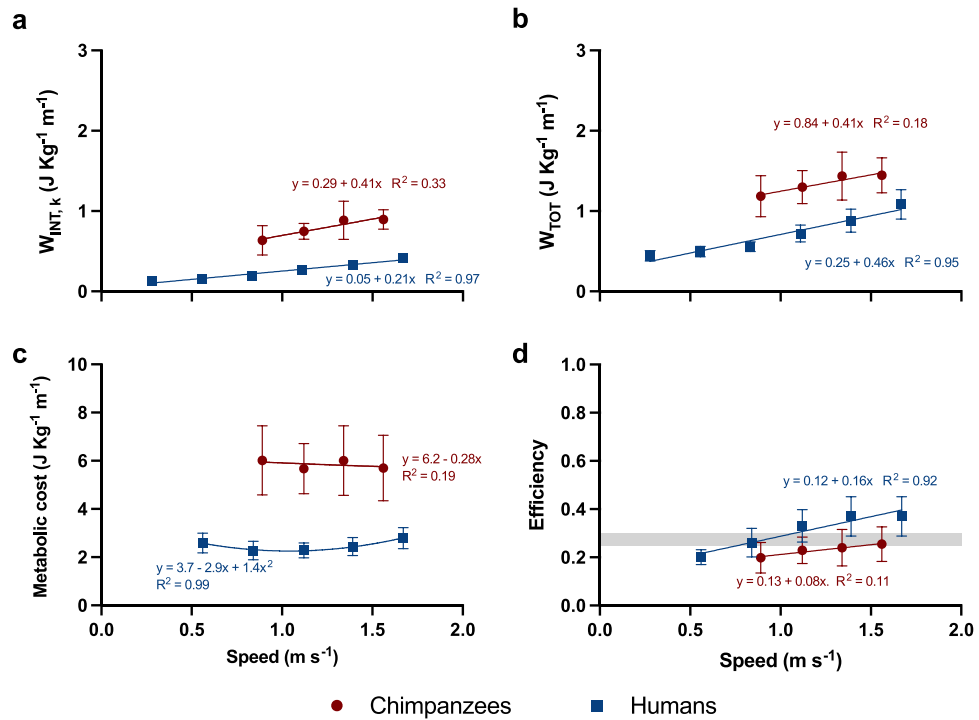


Figure 2. Mechanical work, metabolic cost, and efficiency. Internal kinetic mechanical work ($W_{INT,k}$), total mechanical work (W_{TOT}), metabolic cost, and locomotor efficiency are plotted as a function of speed. Data from Pavei et al.²⁹ for humans. Error bars: standard deviation. Solid lines: regression lines for chimpanzees (red) and humans (blue). Shaded area in panel (d): maximum efficiency range for isolated muscles contracting concentrically⁴³.

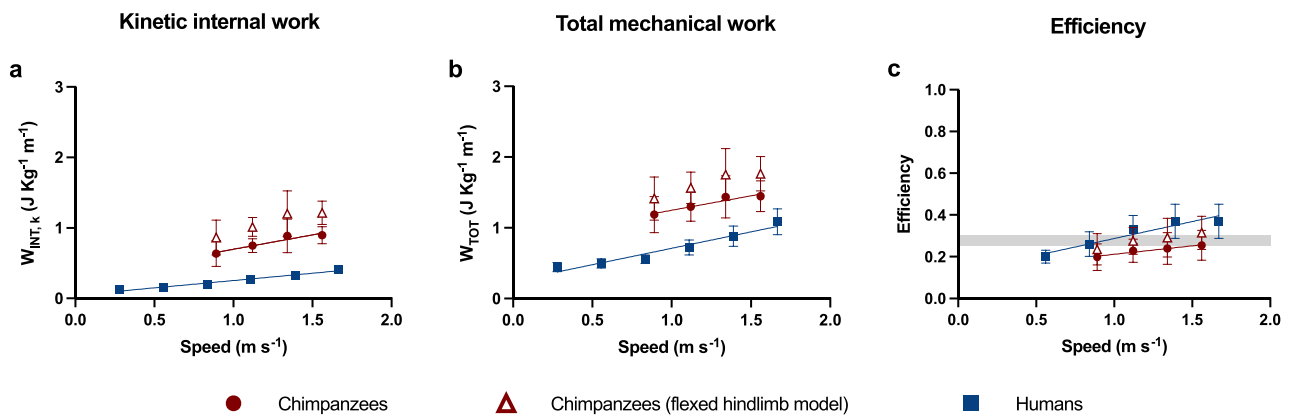


Figure 3. Mechanical work and efficiency assuming a flexed hindlimb. In addition to the data presented in Fig. 2, this plot shows how assuming a flexed lower limb for chimpanzees impacts modeled $W_{INT,k}$, W_{TOT} , and efficiency. In the flexed limb model, a mean knee flexion angle of 125° (with 180° representing knee full extension) and a mean angle of the foot relative to the vertical of 80° was considered (see Supplementary Material S1). Error bars: standard deviation.

great differences in damping coefficients. Therefore, $W_{INT,f}$ was not quantified here or included in W_{TOT} ; this quantity however should not be negligible, and once data on damping become available, estimates of mechanical work in chimpanzees could be improved.

Finally, the interplay between W_{EXT} and $W_{INT,k}$ is not solved yet: summing them could be considered an “upper bound” estimate of whole-body mechanical work^{48,49} and their metabolic correlate may seem counterintuitive since C of human walking increases when people are not allowed to swing their arms⁵⁰. However, the fact that the *net* effect of removing upper limb swing increases C does not imply that limb swing happens at no metabolic cost. On the contrary, muscle blood flow measurements in animal and modeling studies^{51,52}, the existence of dissipation between and within joints³³ and the fact that $W_{INT,f}$ values in humans are of the same magnitude as

those of $W_{\text{INT},k}$ themselves³³ challenge the idea that limb swing can happen at negligible cost and that calculations of limb swing costs can be ignored. Further models should also include the effect of natural limb oscillation frequency^{48,53,54} and $W_{\text{INT},f}$ ³³ on C.

Locomotor efficiency

Due to the lower W_{EXT} ⁶ and $W_{\text{INT},k}$, humans had a lower W_{TOT} : consequently, the disparities in locomotor efficiency between the two species were considerably smaller than those in C (Fig. 2). While this suggests that a portion of the lower C in humans can be attributed to reduced mechanical work, the extant differences in efficiency between the two species hint that mechanical work does not explain all variations in C. Moreover, efficiency was speed-dependent (Fig. 2); for chimpanzees, this was due to the fact that W_{EXT} and C were approximately constant, while $W_{\text{INT},k}$ increased with speed. Finally, differences in W_{TOT} are less pronounced when comparisons are done at dynamically similar speeds (Supplementary Fig. S4).

Locomotor efficiency can also be expressed as the product of muscle efficiency and transmission efficiency⁵⁵, and humans may have optimized both components. Muscle efficiency may be enhanced due to optimized muscle architecture and a higher proportion of type I fibers^{1,4,56}; it also increases when muscles operate at advantageous velocities^{43,57,58}, but data are lacking for chimpanzees walking. On the other hand, transmission efficiency increases when elastic energy is stored and released in the tendons and connective tissues of the hip, ankle, and foot^{59–64}; this can result in overall (“apparent”) efficiency being higher than that of isolated muscle (Fig. 2). Such a hypothesis is supported by observations by O’Neill and colleagues¹⁹ who found that humans, but not chimpanzees, can save a relevant fraction of mechanical work during a stride through elastic mechanisms; this could account for some of the remaining between-species differences in efficiency in Fig. 2. When using mechanical work data from O’Neill and colleagues¹⁹ to compute locomotor efficiency, we found values of 0.23 for chimpanzees and 0.37 for humans walking at 1.09 m s^{-1} (Supplementary Material S5). O’Neill et al.¹⁹ also estimated how much work humans could save due to elastic mechanisms: by subtracting it from total mechanical work, a “muscle” efficiency of 0.25 is derived. At the same speed, our efficiency estimates are 0.22 for chimpanzees and 0.29 for humans (Supplementary Material S5). This suggests numerical consistency between the present results and those from O’Neill and colleagues¹⁹ and that the remaining discrepancies in locomotor efficiency between species can be attributed to factors not captured by mechanical work calculations, including optimized muscle–tendon mechanics in humans. Transmission efficiency also improves when muscles operate at advantageous lengths and moment arms, and with reduced lower limb co-contractions⁵⁵; both mechanisms may contribute to reducing C in humans thanks to their ability to walk with more extended hips and knees^{1,65}. In contrast, the pelvis orientation in chimpanzees forces them to keep these joints bent during the stance phase^{3,14,65}, likely at the cost of increased isometric contraction of lower limb muscles. This can increase C without affecting W_{EXT} . Transmission efficiency also depends on belly and tendon gearing⁶⁶ and soft tissue deformations^{19,67}; further studies are needed to elucidate their role in the comparative physiology of walking.

Limitations and future perspectives

This work relies on published data to estimate differences in $W_{\text{INT},k}$ between humans and chimpanzees and generate hypotheses on how they affect the cost of walking. The present is an analytical estimate of $W_{\text{INT},k}$: the model can yield reasonable estimates since it holds for a range of gaits, speeds, and species^{28,44,45}, but experiments are needed to measure $W_{\text{INT},k}$ in chimpanzees and test these hypotheses by collecting mechanical and metabolic data on the same participants. Experimental measures would also show whether mediolateral movements, which are neglected in this model but are potentially relevant for chimpanzees, affect internal work calculations. Of note, experimental data on W_{EXT} and C come from adult chimpanzees with heterogeneous age and biometry (Table 1); however, chimpanzees’ walking mechanics does not relevantly change after the age of 5 years⁶⁸.

On one hand, further experiments are required to measure quantities that could refine estimates of mechanical work in chimpanzees, including the precise amount of external work done during the double support phase^{69,70}, the mechanical work actually performed at the muscle level^{71,72}, and tendon elastic storage and recoil, which would require combined ultrasound and kinetic data⁵⁹. On the other hand, between-species differences in metabolic cost have also been addressed by force-based rather than work-based models^{3,53,73}; future work may elucidate whether these two contributions are mutually exclusive, additive⁷⁴ or equivalent⁷⁵.

Conclusions

Compared to chimpanzees, the lower cost of human walking is associated with a combined reduction in the work to accelerate and raise their body center of mass and the work to swing their limbs. When both terms are considered, estimated walking efficiency is still higher in humans than chimpanzees, suggesting that factors beyond mechanical work also contribute to such differences in metabolic cost between the two species.

Data availability

No new data was generated for this study.

Received: 9 January 2024; Accepted: 8 April 2024

Published online: 18 April 2024

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Acknowledgements

We thank the anonymous reviewers for their constructive feedback, which improved the manuscript.

Author contributions

FL: conceptualization, methodology, formal analysis, investigation, visualization, writing: original draft, writing: review and editing. LR: conceptualization, methodology, formal analysis, investigation, writing: original draft, writing—review and editing. AM: methodology, writing: review and editing, supervision. GP: conceptualization, methodology, writing: original draft, writing: review and editing, supervision.

Funding

Open Access funding enabled and organized by Projekt DEAL. LR is supported by the Alexander von Humboldt Foundation. We acknowledge the support of the German DEAL Agreement to cover the Article Processing Charges.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-024-59171-8>.

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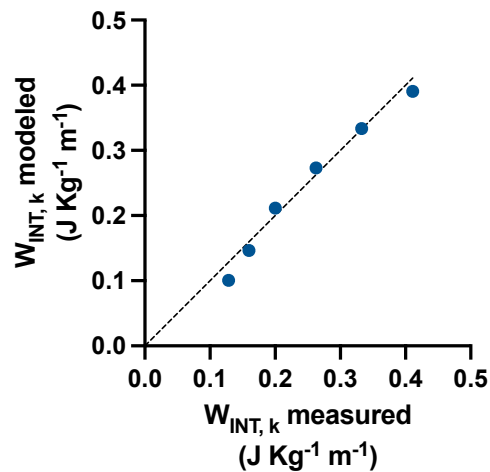
The work to swing limbs in humans versus chimpanzees and its relation to the metabolic cost of walking.

Francesco Luciano*¹, Luca Ruggiero*^{1,2}, Alberto E. Minetti¹ and Gaspare Pavei¹

SUPPLEMENTARY MATERIALS

S1. Validity of the estimates of internal kinetic mechanical work

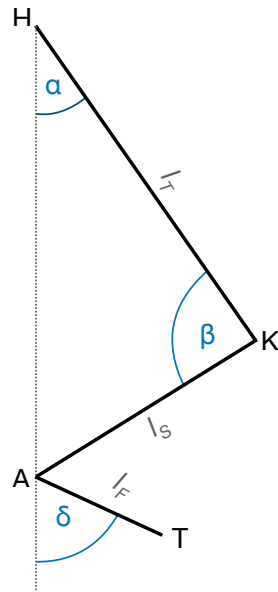
In the present study, the estimated $W_{INT,k}$ for chimpanzees is compared with experimental values for humans. Would these results hold if human values were derived using the same modeling approach? If $W_{INT,k}$ is estimated from the data provided by Pavei and colleagues¹, it aligns closely with its experimental measurements (Supplementary Figure 1). Thus, the utilization of a modeled $W_{INT,k}$ *per se* does not appear to bias the comparisons between chimpanzees and humans.



Supplementary Figure 1. Comparison between measured and modeled $W_{INT,k}$ for human bipedal walking. Calculated from Pavei et al.¹. Dashed line: identity line.

However, such comparisons could still be biased by specific assumptions inherent to the $W_{INT,k}$ model. Minetti's model² assumes equal angular excursion between the upper limb (or forelimb) and lower limb (or hindlimb); such an assumption was not originally tested for chimpanzees but seems reasonable in light of kinematic data collected on such species. For instance, Finestone et al.³ found that chimpanzees walk at their freely chosen speed with a retraction angle of 24 [23 ; 28] degrees (mean [Q1; Q3]) for the forelimb and 27 [24; 31] for the hindlimb, and a protraction angle of 34 [30; 35] degrees for the forelimb and 31 [28; 34] degrees for the hindlimb.

Furthermore, the q' term is calculated under the assumption of fully extended limbs. While this is reasonable for humans, it may not hold for chimpanzees, who exhibit greater knee flexion angles during walking. For context, from O'Neill et al.⁴ we can calculate a mean knee flexion angle of $27 \pm 21^\circ$ for humans and $55 \pm 18^\circ$ for chimpanzees during a stride (0° representing full knee extension). Here we estimate the magnitude and direction of such bias in the $W_{INT,k}$ model. To simplify this analysis, we consider a lower limb that touches the ground at the tip of the foot T and whose knee and ankle are bent throughout the stride with constant angles β and δ , respectively (Supplementary Figure 2).



Supplementary Figure 2. Geometric model of the lower limb. The positions of the hip (H), knee (K), and ankle (A) joints are depicted on the parasagittal angle, while T indicates the position of the tip of the foot. l_T , l_S , and l_F : length of the thigh, shank, and foot segments, respectively.

With the reference frame set at the hip joint, the position of T is:

$$\mathbf{T} : \begin{pmatrix} T_x \\ T_y \end{pmatrix} = \begin{pmatrix} l_F \sin(\delta) \\ -\sqrt{(l_T^2 + l_S^2 + 2l_T l_S \cos(\beta)) - l_F \cos(\delta)} \end{pmatrix} \quad (\text{S1})$$

where l_T , l_S , and l_F are the lengths of the thigh, shank, and foot segments, and the Cosine Rule is applied for the y coordinates. The lower limb length (L_{LL}) is:

$$L_{LL} = \sqrt{T_x^2 + T_y^2} \quad (\text{S2})$$

Defining the distances of the centre of mass for each segment relative to the proximal extremity as RP_T , RP_S , and RP_F for the thigh, shank, and foot, respectively, the positions of CM_T , CM_S , and CM_F are:

$$\mathbf{CM}_T : \begin{pmatrix} CM_{T_x} \\ CM_{T_y} \end{pmatrix} = \begin{pmatrix} RP_T \sin(\alpha) \\ -RP_T \cos(\alpha) \end{pmatrix} \quad (\text{S3})$$

$$\mathbf{CM}_S : \begin{pmatrix} CM_{S_x} \\ CM_{S_y} \end{pmatrix} = \begin{pmatrix} l_T \sin(\alpha) - RP_S \cos\left(\beta + \alpha - \frac{\pi}{2}\right) \\ -l_T \cos(\alpha) - RP_S \sin\left(\beta + \alpha - \frac{\pi}{2}\right) \end{pmatrix} \quad (\text{S4})$$

$$\mathbf{CM}_F : \begin{pmatrix} CM_{F_x} \\ CM_{F_y} \end{pmatrix} = \begin{pmatrix} RP_F \sin(\delta) \\ -\sqrt{[l_T^2 + l_S^2 - 2l_T l_S \cos(\beta)] - RP_F \cos(\delta)} \end{pmatrix} \quad (\text{S5})$$

where $\sin(\alpha)$ and $\cos(\alpha)$ are given by the Sine Rule and the Pythagorean trigonometric identity:

$$\sin(\alpha) = \frac{l_S}{AH} \sin(\beta) = \frac{l_S}{-\sqrt{[l_T^2 + l_S^2 - 2l_T l_S \cos(\beta)]}} \sin(\beta) \quad (\text{S6})$$

$$\cos(\alpha) = \sqrt{1 - \sin^2(\alpha)} \quad (\text{S7})$$

Given m_T , l_T , CM_T the mass, length, and centre of mass for the thigh, m_S , l_S , and CM_S for the shank, and m_F , l_F , and CM_F for the foot, the position of the centre of mass of the lower limb CM_{LL} and its distance from the hip joint (r) are:

$$CM_{LL} = \left(\frac{1}{m_{LL}}\right) [m_T CM_T + m_S CM_S + m_F CM_F] \quad (S8)$$

$$r = \sqrt{CM_{LLx}^2 + CM_{LLy}^2} \quad (S9)$$

The moment of inertia of each segment within the limb relative to their centre of mass I_{TCoM} , I_{SCoM} and I_{FCoM} is given by:

$$I_{TCoM} = m_T g_T^2 \quad (S10)$$

$$I_{SCoM} = m_S g_S^2 \quad (S11)$$

$$I_{FCoM} = m_F g_F^2 \quad (S12)$$

where g_T , g_S and g_F are the radii of gyration of the lower limb segments relative to their centre of mass. The moment of inertia of the lower limb relative to its centre of mass I_{LLCoM} is hence:

$$I_{LLCoM} = I_{TCoM} + \left(m_T \overline{CM_T CM_{LL}}^2\right) + I_{SCoM} + \left(m_S \overline{CM_S CM_{LL}}^2\right) + I_{FCoM} + \left(m_F \overline{CM_F CM_{LL}}^2\right) \quad (S13)$$

where $\overline{CM_T CM_{LL}}$, $\overline{CM_S CM_{LL}}$ and $\overline{CM_F CM_{LL}}$ are the distances between the centre of mass of the thigh, shank, and foot, and the centre of mass of the lower limb (according to the Parallel Axis Theorem). The equations above can also be applied to the upper limb to determine the position of the centre of mass CM_{UL} , length L_{UL} , and moment of inertia relative to the centre of mass I_{ULCoM} . In this special case, however, it can be assumed that $\alpha = \beta = \delta = 0$. Finally, L , a and g can be differentially calculated for the extended lower limb (L_{LLE} , a_{LLE} , g_{LLE}), flexed lower limb (L_{LLF} , a_{LLF} , g_{LLF}), and extended upper limb (L_{ULE} , a_{ULE} , g_{ULE}) and $W_{INT,k}$ can be recalculated by generalizing Equation 9 as:

$$W_{INT,k} = SF v_{ST} \left(1 + \left(\frac{d}{1-d}\right)^2\right) \frac{\pi^2}{4} \left[\left(m'_L a_{LLE}^2\right) + \left(m'_U a_{ULE}^2 \frac{L_{ULE}^2}{L_{LLE}^2}\right) + \left(m'_L \frac{g_{LLF}^2}{L_{LLF}^2}\right) + \left(m'_U \frac{g_{ULE}^2}{L_{LLE}^2}\right) \right] \quad (S14)$$

This equation can be solved to produce the values illustrated in Figure 3. Inertial parameters were taken from Druelle et al.⁵ and Winter⁶, with a mean value of β of 125° ($180^\circ-55^\circ$), and of δ of 81° from O'Neill et al.⁴. Accounting for flexed lower limb is expected to increase $W_{INT,k}$. Such increase occurs because on one side hindlimb gyration radius decreases in chimpanzees, but on the other side the decreased hindlimb length increases at a given speed and stride frequency the angular acceleration and the rotational kinetic energy requirements, with almost constant translational work. This would also cause a slight increase in W_{TOT} and efficiency for chimpanzees: discrepancies in efficiency between species would be slightly lower, and a higher proportion of the differences in metabolic cost would be explained by variations in mechanical work. In conclusion, lower limb flexion may account for some of the remaining variations in efficiency observed between humans and chimpanzees in Figure 2; however, its impact is relatively small compared with the disparities in metabolic cost and mechanical work between the two species. The assumption of a straight lower limb gives a simple and conservative estimate of mechanical work and is therefore used in the main text for the sake of clarity.

S2. Model for $W_{INT,f}$ with different damping and length for upper and lower limbs

In Minetti et al.⁷ the mechanical cost of transport to overcome the internal friction of a single limb (C_{mif} , $J m^{-1}$) and the mass-specific mechanical cost to overcome the internal friction of all four limbs (C_{mifa} or $W_{INT,f}$, $J kg^{-1} m^{-1}$) were given by:

$$C_{mif} = \frac{\pi^2 \beta}{8 R_L^2} v \quad (S15)$$

$$C_{mifa} = W_{INT,f} = \frac{\pi^2 B}{8 m R^2} v \quad (S16)$$

with

$$B = \sum_{i=1}^4 \beta_i \quad (S17)$$

where β_i are the damping coefficients ($N m s rad^{-1}$) of each proximal limb joint. This equation assumes that the four limbs have the same length R . However, this assumption may limit

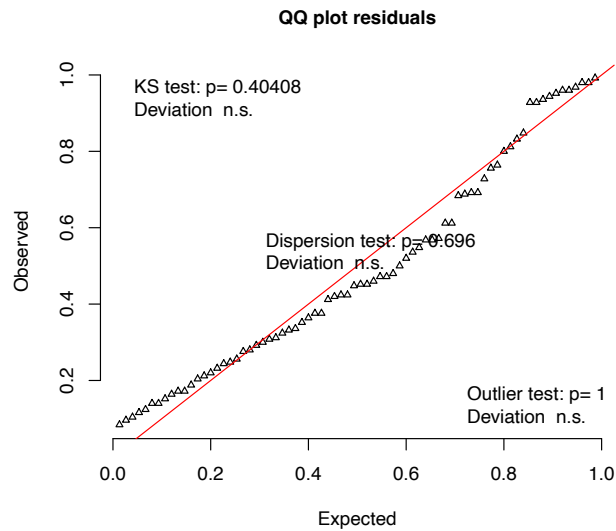
comparisons across species with different upper limb (forelimb) versus lower limb (hindlimb) length ratios. Hence, C_{mifa} can be alternatively expressed as the sum of the cost to overcome the internal frictions of the two upper limbs (or forelimbs) C_{mifU} and the cost to overcome the internal frictions of the two lower limbs (or hindlimbs) C_{mifL} :

$$C_{mifa} = W_{INT,f} = \frac{1}{m} (C_{mifU} + C_{mifL}) = \frac{\pi^2 \beta_U v}{m \cdot 8 R_U^2} + \frac{\pi^2 \beta_L v}{m \cdot 8 R_L^2} = \frac{\pi^2}{8 m} v \left(\frac{\beta_U}{R_U^2} + \frac{\beta_L}{R_L^2} \right) \quad (S18)$$

where β_U is the damping coefficient of the upper limbs under unloaded swinging, and β_L is the damping coefficient of the lower limbs given by the sum of their tensile unloaded and compressive loaded damping coefficients⁷. Damping coefficients have been experimentally determined for humans by Minetti et al.⁷; however, their values in chimpanzees are unknown.

S3. Model selection for external mechanical work

To assess the relation between W_{EXT} and speed in chimpanzees, data were fitted with zero-, first-, and second-order mixed effects models. Their Akaike Information Criteria (AIC) were -79.1, -75.0, and -75.5, respectively; hence, the zero-order model was chosen. The distribution of its residuals was checked and reported below (Supplementary Figure 3).



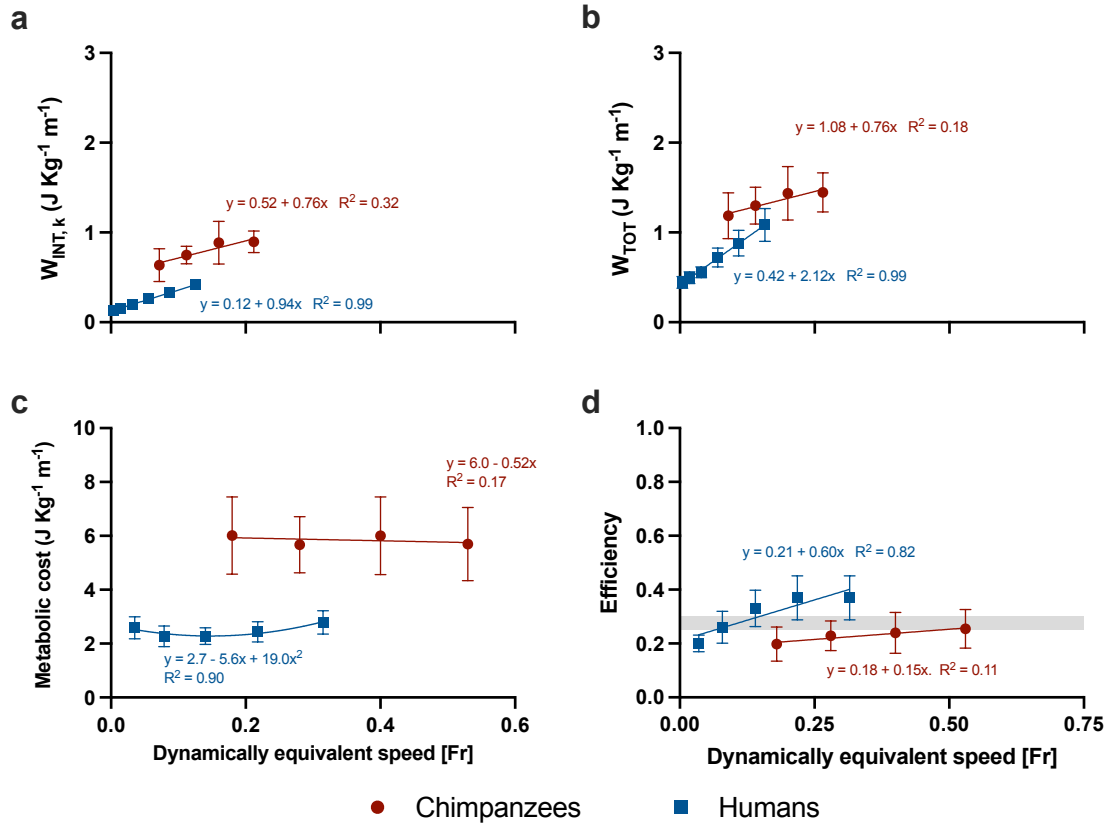
Supplementary Figure 3. Quantile-quantile plot for the observed and expected residuals for the zero-order mixed effects model. The plot and the model checks, included the Kolmogorov-Smirnov (KS) test, the dispersion test, and the outlier test were obtained through the “DHARMA” package in R.

S4. Comparisons of cost, mechanical work, and efficiency at dynamically equivalent speeds

In the main text, mechanical and metabolic variables are compared at absolute speeds; here, they are compared at dynamically equivalent speeds expressed as Froude numbers^{8,9} (Supplementary Figure 4):

$$Fr = \frac{v^2}{g l} \text{ (S19)}$$

where v is the average progression speed (m s^{-1}), g is the gravity acceleration on Earth (9.81 m s^{-2}) and l is the lower limb or hindlimb length (m; chimpanzees: $0.46 \pm 0.05 \text{ m}$; humans: $0.90 \pm 0.03 \text{ m}$; mean \pm standard deviation).



Supplementary Figure 4. Mechanical work, metabolic cost, and efficiency. Internal kinetic mechanical work ($W_{INT,k}$), total mechanical work (W_{TOT}), metabolic cost, and locomotor efficiency are plotted as a function of Froude number (Fr). Data from Pavei et al.¹ for humans. Error bars: standard deviation. Solid lines: linear regression for chimpanzees (red) and humans (blue). Shaded area in panel d: maximum efficiency range for isolated muscles contracting concentrically¹⁰.

S5. Evidence from comparative studies on joint work

In a recent study, O'Neill and colleagues¹¹ compared the dimensionless total mechanical work of the lower limb of three humans and three chimpanzees walking bipedally. This measure differs from the whole-body W_{TOT} calculated in the present paper for two main reasons: first, the total mechanical work from O'Neill and colleagues is given by the summed contributions of the hip, knee, and ankle joint work instead of the summed W_{EXT} and $W_{INT,k}$; second, it was made dimensionless by dividing by $m g l$, where m is the body mass, g is the gravity acceleration, and l is the lower limb

or hindlimb length. This term will hence be referred to as ω_{TOT_JW} . The corresponding dimensional total mechanical work in $J\ kg^{-1}\ m^{-1}$ can be calculated as:

$$W_{TOT_JW} = \omega_{TOT_JW} g l SF v^{-1} \quad (S20)$$

where SF is the stride frequency (Hz) and v is the average progression speed ($m\ s^{-1}$). At a speed of $1.09\ m\ s^{-1}$, ω_{TOT_JW} was 0.27 for chimpanzees and 0.12 for humans. At that speed, a metabolic cost (C) of $5.9\ J\ kg^{-1}\ m^{-1}$ is expected for chimpanzees and $2.20\ J\ kg^{-1}\ m^{-1}$ for humans. If efficiency is then calculated as $W_{TOT_JW} C^{-1}$, this would be equal to 0.23 for chimpanzees and 0.37 for humans. O'Neill et al.¹¹ also estimated how much work humans could save due to elastic storage and release at the tendons and connective tissues of the hip and ankle: by subtracting it from ω_{TOT_JW} , this led to a total 'muscle fiber' work of 0.08, which would correspond to an efficiency of 0.25. At the same speed, our estimates of efficiency are 0.22 and 0.29 for chimpanzees and humans, respectively. This suggests that the results from our paper are coherent with those from O'Neill and colleagues¹¹; it also suggests that the remaining differences in walking efficiency between species can be accounted for by optimized muscle-tendon mechanics in humans.

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