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François Druelle, Jonathan Özçelebi, François Marchal, Gilles Berillon. Analyzing Instantaneous Energy in Bipedal Walking of Baboons: A Model for Exploring the Evolutionary Transition Toward Efficient Bipedalism in Hominins. *American Journal of Biological Anthropology*, 2025, 186 (4), pp.e70056. <10.1002/ajpa.70056>. <hal-05183936>

HAL Id: hal-05183936

<https://hal.science/hal-05183936v1>

Submitted on 29 Jul 2025

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Analyzing instantaneous energy in bipedal walking of baboons: a model for exploring the evolutionary transition toward efficient bipedalism in hominins

Short running title: Analyzing instantaneous energy in baboon bipedalism

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Abstract

Objective: Non-human primates exhibit bipedal walking with a typical “bent-hip, bent-knee” posture, incurring additional energy costs as shown by studies using electromyography and mechanical analysis. During the evolution of habitual bipedalism in hominins, this mode underwent a gradual refinement, culminating in the genus *Homo*. To explore energy conservation mechanisms and the influence of kinematics during occasional bipedal walking, we investigated energy dynamics within different body segments in an ontogenetic sample of baboons.

Materials and Methods: Kinematic and morphometric data from 17 baboons, including mature and immature individuals, were initially collected at the CNRS Primatology station (France). We calculated the potential and kinetic (rotational and translational) energies of various body segments over 40 strides, followed by comparison with human data.

Results: Age-related kinematic differences influence energy recovery percentages in baboons, particularly in the shank and trunk segments. While significant differences can be observed between baboons and humans, such as in the trunk, arm and foot segments, similarities exist in the thigh and shank segments, with the thigh being the primary segment for substantial energy transfer. Unlike humans, baboons lack an optimal speed range for energy recovery.

Discussion: We present a model for energy recovery in flexed bipedal walking. While baboon bipedalism is inefficient in energy recovery, minor trunk motion adjustments could greatly enhance efficiency. These subtle refinements have the potential to increase energy recovery rates, making bipedalism more practical for regular use. From an evolutionary perspective, such improvements would be particularly noteworthy considering other challenging activities like climbing and arboreal quadrupedalism.

Key words: Bipedalism, Kinetic energy, Potential energy, Energy conservation, Primates

Introduction

Exploring the biomechanics of bipedal locomotion in non-human primates raises questions about the factors that contribute to the great efficiency of human bipedal locomotion (e.g., O'Neill, Demes, Thompson, & Uemberger, 2018; O'Neill et al., 2022; Hirasaki et al., 2006; Kimura, & Yaguramaki, 2009; D'Août, Aerts, & Berillon, 2014; Thompson, Demes, O'Neill, Holowka, & Larson, 2015; Machnicki, Spurlock, Strier, Reno, & Lovejoy, 2016; O'Neill et al., 2018; Thompson et al., 2021). Studies have shown that non-human primates face significant challenges when walking upright on two legs (e.g., D'Août et al., 2004; Nakatsukasa, Hirasaki, & Ogihara, 2006; Sockol, Raichlen, & Pontzer, 2007; Demes et al., 2015). When they stand and walk bipedally, their 'bent-hip, bent-knee' posture creates a high flexion moment about the hip and knee (Crompton, Weijie, Günther, & Savage, 1998; Hora, Struska, Matejovska, Kubovy, & Sladek, 2023) that requires greater muscle activation and muscle coactivation in the back and hindlimbs compared to their typical quadrupedal gait (macaques: Higurashi et al., 2019; baboons: Druelle et al., 2024; chimpanzees and orangutans: Shapiro & Jungers, 1994; Stern & Susman, 1981). Regarding metabolic energy costs of bipedal *versus* quadrupedal walking, previous researchers have presented a complex picture. Studies conducted on macaques indicated that the overall metabolic energy cost of bipedal walking is greater than that of quadrupedal walking (Nakatsukasa et al., 2004, 2006). However, other investigations involving two juvenile chimpanzees, two capuchin monkeys and one spider monkey found no significant differences at similar velocities between the two locomotor modes (although it is important to note that these animals could not achieve the same maximal speed during bipedalism compared to quadrupedalism; Taylor & Rowntree, 1973). Additionally, a study on chimpanzees has highlighted that large inter individual variability can exist, adding complexity to our understanding of metabolic energy costs during bipedal and quadrupedal walking (Sockol et al., 2007). Nonetheless, without exception, when compared to human bipedal walking, the energy expenditures (calculated from calorimetry and net external mechanical work) associated with bipedal locomotion in various non-human primate species consistently prove to be higher (see Table 6 in Demes et al., 2015).

During both bipedal and quadrupedal walking in relatively large animals (>1 kg), the movement of the body centre of mass generally follows an inverted pendulum trajectory (Reilly, McElroy, & Biknevičius, 2007), where potential energy and kinetic energy fluctuate out-of-phase, allowing for energy exchange between them. Kinetic and potential energies represent two forms of energy that can be stored and transferred to each other during optimal movement as it is in a simple pendulum (Cavagna, Heglund, & Taylor, 1977; Alexander, 1991). As the centre of mass rises, kinetic energy is converted to potential energy, and during the fall, potential energy is converted back into kinetic energy. Maximal energy recovery (i.e., 100% recovery) occurs when the amplitudes of both energy fluctuations are similar, and

they fluctuate perfectly out-of-phase. Although the total external mechanical energy and energy recovery have been assessed during bipedal and/or quadrupedal walking in different species of non-human primates such as in chimpanzees (Pontzer, Raichlen, & Rodman, 2014; Demes et al., 2015), bonobos (D'Août et al., 2004), gibbons (Vereecke, D'Août, & Aerts, 2006), capuchin monkeys (Demes, & O'Neill, 2013), baboons (Druelle et al., 2021), macaques (Cavagna et al., 1977; Ogihara, Makishima, Hirasaki, & Nakatsukasa, 2012) and ring-tailed lemur (Schmitt, 2011), no study has explored the energy exchange within body segments and their contributions to the total energy changes during the walking strides. Yet, the body is composed of articulated segments, and covering a given distance can be done efficiently or in various inefficient ways. Therefore, segmental mechanical energy analysis can reveal how energy flows between segments and how the mechanical energy pattern of the body centre of mass relates to the underlying energy mechanisms in the lower limb segments. This type of analysis has provided valuable insights into human movement (e.g., Cappozzo, Figura, Marchetti, & Pedotti, 1976; Winter, Quanbury, & Reimer, 1976; Winter, & Robertson, 1978; Mansour, Lesh, Nowak, & Simon, 1982; Hof, Nauta, van der Knaap, Schallig, & Struwe, 1992; Bianchi, Angelini, Orani, & Lacquaniti, 1998; Miller & Verstraete, 1999). For instance, the analysis of the energy exchange within body segments has shown that the trunk is a very conservative system that undergoes important energy exchange. Similarly, the thigh represents a segment that exhibits energy conservation during bipedal walking. On contrary, the shank does not show energy recovery through an optimal transfer between kinetic and potential energy (Winter et al., 1976). Instead, it relies on elastic energy storage thanks to the presence of a well-developed Achilles tendon (e.g., Butler, & Dominy, 2016; Aerts, D'Août, Thorpe, Berillon, & Vereecke, 2018). As seen in humans, evaluating where energy is conserved during occasional bipedal walking in non-human primates, and where there is no energy exchange, can provide insights into the intrinsic (energetic) nature of the bipedal locomotion and help to better identify the anatomical regions that need to be refined to master bipedalism (e.g., Machnicki et al., 2016; O'Neill et al., 2022). From an evolutionary perspective, since these primates walk with flexed postures, one can hypothesize that the *Pan/Homo* last common ancestor (LCA) also adopted a flexed bipedal posture. In this context, one might wonder about the patterns of energy exchange within body segments during “bent-hip, bent-knee” walking. Answering this question could provide new insights into the shift toward a more extended posture.

Previous observations indicate that the kinematics of bipedal walking in primates undergo slight changes with age, potentially associated with modifications in body mass distribution and motor control strategies (see Druelle, Özçelebi, Marchal, & Berillon, 2022, in olive baboons; and Kimura, 1996; Kimura & Yaguramaki, 2009, in chimpanzees). In baboons and macaques, there is a posterior shift in the total centre of mass and a proximal shift in the centre of mass of the limbs (Druelle, Aerts, D'Août,

Moulin, & Berillon, 2017; Raichlen, 2005; Turnquist, & Wells, 1994). While these changes in the morphotype may align with their specialization for efficient quadrupedal walking, they can also influence patterns of energy exchange during bipedal locomotion. In concrete terms, juvenile baboons typically have a slightly more erect trunk compared to adults (as also observed in chimpanzees) and a more vertically oriented shank segment (i.e., a smaller segment angle relative to the horizontal; Druelle et al., 2022). Their movement adjustments differ from adults, with a greater hip amplitude in general and a reduced knee amplitude as speed increases (young chimpanzees exhibit a greater extension in the hip joint and a larger range of motion compared to adults; Kimura & Yaguramaki, 2009). This developmental aspect provides an opportunity to use ontogenetic changes (including morphotype and kinematics) as a natural experiment (see Hurov, 1991) to test the potential impact on energy exchange in occasional “bent-hip, bent-knee” bipedal primates.

Our study aims to analyze the energy components of mature and immature baboon bipedal gait in the sagittal plane, focusing on steady ground locomotion, to identify conservation of mechanical energy. Such an approach, quantifying the instantaneous energy patterns of linked-segment movements, has been previously applied in humans (e.g., Winter, 1976; Bianchi et al., 1998), providing important conclusions about walking. Exploring the bipedal walking pattern of the baboon in this context is relevant due to its typical flexed posture, which is similar to other non-human primates but dissimilar to humans (D'Août et al., 2014; Druelle, & Berillon, 2014; Rosen, Jones, & DeSilva, 2022). It thus brings valuable insights into the influence of such a posture on mechanical energy conservation during bipedal locomotion. To investigate where baboons store and release energy during occasional bipedal walking, we calculated the instantaneous potential and kinetic (translational and rotational) energy of the body segments, as well as the energy of the body centre of mass. Firstly, the comparison between immature and mature baboons aimed to investigate the impact of the different morphological patterns and kinematic strategies previously observed (Druelle et al., 2017; 2022) on energy exchange among segments. Specifically, considering the distinct control strategies observed at various speeds, we anticipate that mature baboons might exhibit slightly different energy exchange patterns than immature individuals. Secondly, a comparative analysis was conducted between mature baboons and a sample of adult humans. The objective is to evaluate the disparity in energy exchange patterns between baboons, which walk with flexed hindlimbs, and humans, who walk with extended hindlimbs.

Undoubtedly, baboons are specialized for quadrupedalism. Despite their inherent specificities, this comparative model can provide valuable insights into how a quadrupedal primate naturally addresses the challenge of walking bipedally with a flexed posture (see D'Août et al., 2014; King, 2022, 2024). Through this comparative and experimental approach, we aim to enhance our understanding of the energetics of bipedal walking in primates, thereby opening new evolutionary perspectives.

Materials and methods

Baboon sample

The raw morphometric and kinematic data used for this study were previously published for other research purposes (Druelle et al., 2017, 2022). The main sagittal joint kinematics were collected using a motion analysis system (high-definition digital video camera, 200 fps, 1280 x 800 pixels resolution, Baumer HXC13) at the CNRS primatology station, where olive baboons, *Papio anubis*, were recorded walking steadily on a straight and horizontal calibrated walkway (see Berillon et al., 2011). Anatomical reference points were digitized using the *DLTdv8* application developed in *MATLAB* by the T. Hedrick Lab (Hedrick, 2008). Data were filtered per stride using a 4th order zero phase shift Butterworth low-pass filter with a cut-off frequency of 10Hz. Associating the tracking of the joints and body segments during the walking strides to the individual morphometrics allowed us to estimate the position of body segments and the body centre of mass (BCoM; kinematic method: Maus, Seyfarth, & Grimmer, 2011). Morphometrics were collected on the same individuals under anaesthesia, and the geometric model of Crompton, Li, Alexander, Wang, & Gunther (1996) was used to estimate the segment mass, centre of mass and inertia. The weighted arithmetic mean centre of mass of all segments permits estimation of the instantaneous position of the BCoM. We estimated the average speed per stride from the derivative of the horizontal displacement of the BCoM. Studies on the growth pattern of baboons have shown that substantial morphological changes occur during the first two years of life and that neuromotor maturation is complete by three years of age in baboons and other cercopithecoids (Dunbar, & Badam, 1998; Druelle et al., 2017; Leigh, VandeBerg, Williams-Blangero, & Tardif, 2009; Rose, 1977; Vilensky, & Gankiewicz, 1990). We previously showed that, from the age of three onward, baboons exhibit a very similar kinematic pattern during bipedalism (Druelle et al., 2022). Therefore, we considered individuals in our sample under three years of age as immature, while those above this age are considered mature. The total dataset comprises 21 strides among 7 immature individuals and 19 strides from 10 mature individuals (Table 1). Figure 1 shows the workflow of the present study. Importantly, the morphometrics and kinematics data are sourced from the same individuals for 7 subjects (within 5 months). In cases where morphometric data for the specific individual studied in the kinematic analysis were unavailable (10 individuals), data from another individual of similar size (within 0.150 kg for immature and 1.7 kg for mature individuals) and age range (within 3 months for immature and 2 years for mature individuals) were used. In this way, the closely matched age and body mass ensured an accurate analysis of their centre of mass movement. Experiments were approved by the Regional Ethical Committee for animal experimentation of the Midi-Pyrénées Region (Letter MP/01/15/02/08).

TABLE 1. Individual data for kinematic recordings of bipedal walking, including associated morphometric measurements taken at the same age (within five months of kinematic tracking), or from an individual of the same sex, within the same age and body mass range.

<i>Kinematics</i>					<i>Morphometrics</i>		
Individual	Sex	Age	Age-class	Number of strides	Corresponding individual*	Age	Body mass
Espiègle	F	1.2	Immature	6	Elvidge	1	3.54
Falbala	F	0.7	Immature	3	Elvidge	0.53	2.3
Filosophie	F	1	Immature	2	Dopram	1.1	3.51
Fleur	F	0.7	Immature	4	Dictée	0.51	2.65
Ford	M	0.6	Immature	2	Djumbo	0.83	2.87
Grant	M	0.5	Immature	1	Dardar	0.44	2.21
Goloum	M	1.4	Immature	3	Dédé	1.31	3.89
Chantal	F	4.1	Mature	2	Chantal	3.85	11.43
Dérive	M	3.8	Mature	1	Dérive	3.88	12.48
Désastre	M	3.5	Mature	3	Désastre	3.35	10.68
Elfira	F	3.5	Mature	1	Elfira	3.63	10.4
Emeraude	F	3.4	Mature	2	Emeraude	3.51	8.36
Epine	F	3.4	Mature	2	Epine	3.13	8.66
Baby	F	6.5	Mature	4	Baby	6.04	12.36
Urbaine	F	7.2	Mature	2	Carbone	5.1	11.31
Ursuline	F	7.4	Mature	1	Chantal	5.65	14.63
Vanessa	F	6.9	Mature	1	Clara	6.11	14.18
Summary	Total	Mean		Total		Mean	Mean
	4F; 3M	0.87	Immature	21		0.82	3.00
	8F; 2M	4.97	Mature	19		4.43	11.45

*Corresponding individual: if morphometric data for the individual studied in the kinematic analysis were unavailable, data from another individual of the same size and age range were used, hence not specifically the exact same age

Human sample

The kinematic data used in this study were obtained from an open dataset (Lencioni, Carpinella, Rabuffetti, Marzegan, & Ferrarin, 2019); a subsample of 31 healthy adult subjects (>15 years old) during level walking at different velocities was analyzed. A total of 607 strides were included in the analysis. The 2D coordinates (X, Y) of 17 external markers on the right and left sides were extracted: Toe1, Heel, Lateral malleoli, Shank (in the centre of the segment), Lateral femoral condyles, Thigh (in the centre of the segment), Anterior superior iliac spine (ASIS), Shoulder (at the acromion), Elbow (lateral epicondyle), Wrist (distal ulna), and Right cheekbone on the head. The speed of progression of every stride (estimated from the linear distance travelled by the hip joint centres' midpoint and provided in the opendataset), the stride length, and the height of the subjects were also extracted. Additionally, the 2D coordinates (X, Y) of the BCoM, available in the open dataset and estimated using a segmental analysis method from Lencioni et al. (2019), were extracted. To complete this dataset, additional

morphometric data were required (segment mass, centre of mass and inertia). We used average morphometric information from Clauser et al. (1969) and Chandler et al. (1975), as provided in Robertson et al. (2004).

Analyses

As baboons differ in size between immature and mature individuals, and mature baboons are smaller than adult humans, we corrected for this effect by scaling the speed following the common scaling procedure (Hof, 1996):

$$\text{Dimensionless speed} = \frac{v}{\sqrt{g * l}}$$

Where g is the gravitational acceleration (9.81 m s^{-2}) and l is the length of the shank, directly measured in baboons and measured in humans as the absolute distance between the lateral femoral condyle and the lateral malleolus provided in Lencioni et al. (2019). As this value may slightly vary ($\sim 1 \text{ cm}$ max) within the stride cycle, we calculated an average value per subject. Using the length of the shank has been shown to be a reliable and appropriate scaling procedure in primate locomotion studies (Aerts, Van Damme, Van Elsacker, & Duchene, 2000; Alexander, 2004; Berillon et al., 2010; Druelle et al., 2022; Isler, & Thorpe, 2003; Vereecke et al., 2006). However, effective limb length is also a common metric in biomechanics (e.g., O'Neill et al., 2022; Pontzer et al., 2014; Ogihara et al., 2018). Hence, for future comparative purposes, we also estimated dimensionless speed in baboons using effective limb length as the scaling factor. Effective limb length is calculated based on the height of the hip at midstance (see Supplementary Table 1), but this calibration could not be applied in the present human sample because the hip joint coordinates were not provided in the marker set of Lencioni et al. (2019).

As conducted in Winter (1976), the variations in translational kinetic (KE_T), rotational kinetic (KE_r) and potential (PE) energies were estimated for the different body segments (si), as follows (see also Cavagna & Kaneko, 1977):

$$KE_T = \frac{1}{2} M_{si} (\dot{Z}^2 + \dot{X}^2)$$

$$KE_r = \frac{1}{2} I_{si} \omega^2$$

$$PE = M_{si} g Z$$

Where M_{si} is the mass of the segment considered, \dot{Z} is the vertical linear velocity of the body segment considered in the sagittal plane and \dot{X} is the linear velocity in the fore-aft direction, I_{si} is the inertia of the segment considered about its centre of mass, ω is the angular velocity of the segment in the sagittal

plane, g is the gravitational acceleration, and Z is the instantaneous height of the segment CoM considered (relatively to the toe when on the ground). We also calculated the variations in kinetic (translational) and potential energy of the BCoM.

The instantaneous total mechanical energy per segment is calculated by summing the potential, the rotational kinetic, and the translational kinetic energies. To reduce noise in the total energy, a 4th-order zero phase shift Butterworth low-pass filter with a cut-off frequency of 10Hz is applied at this stage. It is then possible to estimate the total cost per bipedal stride in two ways (see equations in Figure 1):

1) The total maximal energy can be estimated assuming that no energy transfer happened between segments and that no elastic recovery occurs (see Aerts et al., 2023). Therefore, the instantaneous power is calculated per segment, i.e., the time differential of the energy yields the instantaneous power fluctuations of the segment considered.

2) The total (minimal) energy can be estimated assuming that there is energy transfer and conservation between body segments. The instantaneous power is calculated directly for the full body by summing all the instantaneous total mechanical energy of the different segments.

Then, for power input we assumed an efficiency of 25% (maximal efficiency of the conversion of chemical energy into positive mechanical work; see Cavagna et al., 1977) and for negative power, the efficiency is -100% (see Alexander, 2003). Instantaneous metabolic power is calculated per segment (1) and then summed over all segments (in this way we consider that muscle activation is producing all the mechanical energy needed), or directly for the full body (2). The time integral of the total instantaneous power yields an estimate of the metabolic energy costs for the considered stride cycle. We calculate the cost of transport by dividing the total maximal energy during a stride by the horizontal distance travelled (stride length) and the body mass. To validate this methodology, we calculated the cost of transport in our human sample. As energy transfer is assumed in humans (e.g., Bianchi et al., 1998), we provided the total energy estimated from 2) and compared it with values obtained from the literature.

We estimated the percentage of energy recovery per body segment (foot, shank, thigh, trunk, arm and forearm) and of the BCoM to evaluate the efficiency of the pendular exchange of energy (Heglund, Cavagna, & Taylor, 1982). It is estimated as follows:

$$Recovery (\%) = \frac{\Delta^+PE + \Delta^+KE - \Delta^+TE}{\Delta^+PE + \Delta^+KE} \times 100$$

Where Δ^+PE , Δ^+KE , Δ^+TE are the sum of the positive increments of the potential, translational kinetic, and total energy, respectively, within a bipedal stride. Note that the rotational kinetic energy

was not included in these calculations because the value of the segment angular momentum is marginal compared to the linear momentum (see Results).

Statistical analyses

In order to meet the assumptions of normality and homoscedasticity, the data were log-transformed prior to analysis. This transformation also helped to improve the distribution of the residuals in the models that were tested, as confirmed by Shapiro-Wilk tests applied on the residuals. Initially, mixed effects models were applied to account for individual effects, with individuals treated as random factors. In this case, we used the *lmer* function in the R package *lme4* (Bates et al., 2015) and the Satterthwaite's approximation method implemented in the *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017) to test the significance of the fixed effect variables. However, if it was observed that all of the random effect variance resided in the residual term, a simpler analysis of covariance (ANCOVA) was used. This approach also facilitated better distribution of residuals in the models used for analysis.

First, we tested the influence of age-class (immature *versus* mature) on minimal and maximal cost of transport and on percentage of energy recovery of the BCoM and body segments in baboons (foot, shank, thigh and trunk; dependent variables), while accounting for the effect of (dimensionless) speed as an independent variable. The interaction between the age-class and the speed is included in all tests.

Second, to compare the human and baboon samples, the same dimensionless speed range was considered for both species, and the energy recovery of the BCoM and each body segment was compared using one-sample t-tests, with the mean value of the human sample used as the reference value. The distribution of the data was tested using the Shapiro-Wilk test before applying the one-sample t-test.

Additionally, a multiple linear regression model was applied to assess the relationship between the percentage of energy recovery of the BCoM and the energy recovery of the body segments. The same model was run in baboons and in humans to detect the most significant predictors of the general pattern of energy recovery in both species. All statistical analyses were conducted using R (version 4.0.3) and a significance level set at 0.05.

Results

Assessing cost of transport from instantaneous mechanical energy in humans

Based on kinematics and morphometrics, we estimated the cost of transport in the present human sample as a validation of the methodology used in baboons. This calculation assumes energy transfer

is present, and we obtained a value of $3.14 \pm 0.76 \text{ J kg}^{-1} \text{ m}^{-1}$ in adult humans (>15 years old) at an average speed of $1.19 \pm 0.15 \text{ m s}^{-1}$ (Supplementary Figure 1). This result is very similar to common estimations of the cost of transport in humans ($\sim 3.5 \text{ J kg}^{-1} \text{ m}^{-1}$) obtained from other, more direct respirometry methodologies (e.g., De Graaf, Hubert, Houdijk, & Bruijn, 2019; Gast, Kram, & Riemer, 2019).

Bipedal walking in baboons: immature versus mature individuals

The cost of transport, estimated from kinematics and morphometrics datasets, stands at $9.88 \pm 4.46 \text{ J kg}^{-1} \text{ m}^{-1}$ for immature baboons and $9.66 \pm 2.37 \text{ J kg}^{-1} \text{ m}^{-1}$ for mature baboons when no energy transfer or recuperation is expected. Hence, these estimates represent maximal costs. When estimating the cost of transport assuming energy transfer similar to humans, we obtained values of $3.63 \pm 1.59 \text{ J kg}^{-1} \text{ m}^{-1}$ for immature baboons and $4.00 \pm 1.16 \text{ J kg}^{-1} \text{ m}^{-1}$ for mature baboons. Calculating the net external mechanical work yielded values of $0.73 \pm 0.41 \text{ J kg}^{-1} \text{ m}^{-1}$ and $0.75 \pm 0.25 \text{ J kg}^{-1} \text{ m}^{-1}$ for immature and mature baboons, respectively.

There is a significant effect of speed on the maximal and minimal cost of transport and on the percentage of energy recovery of the BCoM ($P < 0.0001$, $P = 0.002$ and $P = 0.002$, respectively; Table 2). There is a significant effect of age-class on the maximal cost of transport ($P = 0.008$), but there is no age-class effect on minimal cost of transport and the percentage of energy recovery of the BCoM. The interaction effect observed for the maximal cost of transport suggests that immature baboons experience a greater increase to the cost of bipedal walking with speed than mature individuals do ($P = 0.044$; Figure 2). The comparisons of the percentage of energy recovery for each body segment show that there are significant differences for the shank and the trunk segments between age-classes ($P = 0.026$ and $P = 0.034$, respectively; Figure 3A,C). Overall, speed has a significant negative effect on energy recovery on all segments except the forearm (see Table 2 and Figure 3A-F).

Translational kinetic energy and gravitational potential energy are the main energies in play in baboons, while the rotational kinetic energy is very low (see Figure 4).

Baboons versus humans when walking in the same dimensionless speed range

If energy transfer is present in baboons similarly to humans, they would use a comparable amount of energy to move bipedally as humans do (minimal cost of transport at dimensionless speeds between 0.6 and 1.1: $3.57 \text{ J kg}^{-1} \text{ m}^{-1}$ in baboons and $3.70 \text{ J kg}^{-1} \text{ m}^{-1}$ in humans; $t = -0.55$, $df = 12$, $P = 0.59$).

Energy exchange is estimated by the percentage of energy recovery per segment, where 0% indicates no energy exchange (kinetic and potential energy fluctuate perfectly in-phase) and 100% indicates a perfect energy exchange (kinetic and potential energy fluctuate entirely out-of-phase). There is almost no energy exchange in the shank segment and there is no significant difference between baboons and

humans when walking in the same speed range (5.34% and 4.31%, respectively; $t=0.98$, $df=12$, $P=0.35$; Figure 5). Instead, there is an important in-phase fluctuation. The foot also corresponds to in-phase fluctuations of energies, but there is a significant difference between baboons and humans (5.77% and 8.87%, respectively; $t=-5.93$, $df=12$, $P<0.0001$; Figure 5). The thigh segment exhibits periods during which potential and translational kinetic energy are asynchronous (31.79% in baboons and 30.40% in humans). There is no significant difference between humans and baboons ($t=0.35$, $df=12$, $P=0.73$; Figure 5). There is a significant difference for the arm segment (18.91% in baboons and 48.27% in humans; $t=-6.56$, $df=12$, $P<0.0001$; Figure 5), but no significant difference for the forearm segment (22.32% in baboons and 27.81% in humans; $t=-1.83$, $df=12$, $P=0.09$; Figure 5). The most striking difference is in the trunk segment. While there is 32.71% energy exchange in this segment in humans, there is only 0.55% energy exchange in baboons ($t=-289.49$, $df=12$, $P<0.0001$; Figure 5). Finally, the energy recovery of the BCoM is much higher in humans compared to baboons (52.13% and 18.93%, respectively; $t=-13.11$, $df=12$, $P<0.0001$; Figure 6). We also observe that in humans there is an optimal speed range that allows up to 70% energy recovery. Instead, there is no optimal speed range in baboons and energy recovery decreases with speed.

Overall model of energy recovery in baboons and humans

Testing the influence of the energy recovery of all body segments with the resulting energy recovery in the BCoM in baboons reveals that the trunk segment has a very small contribution in absolute terms, but it is significantly related to total energy recovery. We obtained the following multiple linear regression model for energy recovery (ER):

Baboon BCoM ER

$$= 14.34 \times \text{Trunk ER} + 0.27 \times \text{Thigh ER} - 0.5 \times \text{Shank ER} + 0.22 \times \text{Foot ER} \\ + 0.08 \times \text{Arm ER} + 0.15 \times \text{Forearm ER} - 0.53$$

This model (*adjusted R*² = 0.82) shows that baboons could significantly increase their total energy recovery at the level of the BCoM by only slightly improving the movement of the trunk ($P=0.014$). For instance, they would increase their total energy recovery by 14% for every 1% increase in trunk energy recovery. Slightly increasing the conservation of energy in the trunk has the potential to substantially increase the total energy recovery in baboons when they walk bipedally. Testing a similar model in humans (*adjusted R*² = 0.40) reveals that multiple body segments are involved in the total recovery of energy. We obtained the following multiple linear regression model for energy recovery (ER):

Human BCoM ER

$$= 0.36 \times \text{Trunk ER} + 0.09 \times \text{Thigh ER} - 0.43 \times \text{Shank ER} + 0.05 \times \text{Foot ER} \\ + 0.29 \times \text{Arm ER} - 0.14 \times \text{Forearm ER} + 28.16$$

While the trunk is also a significant component in this model ($P < 0.0001$), its contribution is in combination with the shank ($P = 0.0003$), arm ($P < 0.0001$) and forearm ($P = 0.0001$).

DISCUSSION

We investigated the dynamics of energy storage and release in baboons during occasional bipedal walking and found that energy transfer patterns operating in the hindlimb are similar to those observed in humans (e.g., Cappozzo et al., 1976; Winter et al., 1976; Winter, & Robertson, 1978; Mansour et al., 1982; Bianchi et al., 1998). The thigh is the primary segment of substantial energy transfer, while shank movement suggests in-phase fluctuations of energy (see Figure 4). The present estimates for the minimal and maximal cost of transport in baboons are between $3.5 \text{ J kg}^{-1} \text{ m}^{-1}$ and $\sim 10 \text{ J kg}^{-1} \text{ m}^{-1}$. The net external mechanical work ($0.73\text{-}0.75 \text{ J kg}^{-1} \text{ m}^{-1}$) closely corresponds to those observed in gibbons ($0.72 \pm 0.29 \text{ J.kg}^{-1}.\text{m}^{-1}$, Vereecke et al., 2006; see also Table 6 in Demes, Thompson, O'Neill, & Umberger, 2015 for a summary).

Regarding the recovery rate of the BCoM, the range is between 2-42% and 6-43% in immature and mature baboons, respectively. This level of energy recovery is lower than that observed during quadrupedal walking in the same species: 19-53% (recalculated from Druelle et al., 2021 using the same filtering process as in the present study). Energy recoveries during bipedalism in baboons are higher than those found in capuchin monkeys (2-17%, Demes, & O'Neill, 2013) and appear comparable to those observed in chimpanzees (2-45%, Demes et al., 2015; 15-35% and 10-30%, Kimura, & Yaguramaki, 2009). These values are lower than those in macaques (6-62%, Ogihara et al., 2010) and gibbons (10-60%, Vereecke et al., 2006). Note that important variation and overlap can be observed within and between species.

Immature versus mature baboons

We compared occasional bipedal walking in immature and mature baboons. While the energy recovery of the BCoM remains consistently low and exhibits no age-related variation, there is a difference in the estimated maximal cost of transport. Specifically, the cost is slightly, yet significantly, higher in immature compared to mature individuals. Furthermore, the cost exhibits a relatively more pronounced increase with speed in immature baboons than in their mature counterparts. This result is likely linked to the distinct kinematic strategy employed by immature baboons, characterized by an overall higher amplitude of movement in the hip and thigh, along with a longer duty factor. In contrast, mature baboons exhibit a decrease in duty factor with increasing speed, accompanied by an increase in knee amplitude compared to immature baboons (Druelle et al., 2022). The suggested “blocking

strategy” reported in immature baboons in our previous study, as opposed to the “lower leg strategy” of mature individuals, is likely a contributing factor in the observed energetic difference.

In terms of energy transfer patterns during bipedal walking, baboons exhibit similar trends in their thigh, foot, arm, and forearm segments across age groups. Notably, significant differences emerge in the trunk and shank segments, although these differences are not highly pronounced in absolute values. It is noteworthy that energy recovery in the trunk is greater at lower speeds in immature baboons, whereas the speed of progression has no influence on energy recovery of this segment in mature individuals. In other words, the trunk is kept very stable in adult baboons.

Only a limited number of studies have specifically investigated the ontogeny of occasional bipedalism in non-human primates (Kimura, 1991, 1996; Kimura, & Yaguramaki, 2009; Wright, & Fragaszy, 2021; Druelle et al., 2013, 2016, 2017, 2022). Kimura (1996) showed that in chimpanzees the rate of energy recovery increases with age during bipedal walking until the age of four, at which point it stabilizes. The low rates of energy recovery observed in juvenile chimpanzees (~15% vs 30.4% between 5 and 8 years old) are attributed to their inability to consistently lift their centre of mass high enough during the single leg stance phase, resulting in low potential energy. Druelle et al. (2016) and Wright and Fragaszy (2021) quantified the bipedal behaviors of captive olive baboons and free-ranging bearded capuchins, respectively. While the former found age-related differences in the use and proportion of bipedal behaviors, the latter did not observe differences in the frequency of this behavior. Other studies on the ontogeny of positional repertoires have indicated a reduced use of occasional bipedal behavior with increasing age in various primate species (chimpanzees: Sarringhaus et al., 2014; Doran, 1992; gorillas: Doran, 1997; macaques: Wells, & Turnquist, 2001). It is interesting to note that non-human primates quickly adopt bipedal behaviors during their lifespan, demonstrating diverse patterns between species. Potential factors contributing to these variations may include size and allometry, such as changes in body mass distribution (Druelle et al., 2016; Videan, & McGrew, 2002). The ecological relevance of such behavior should also be considered, especially because non-human primate species lack anatomical adaptations for bipedalism but possess a generalist morphology that allows occasional use. For instance, adult capuchins use bipedalism for carrying stones and cracking nuts on the ground (Liu et al., 2009; Mangalam et al., 2018), orangutans utilize it for negotiating flexible branches (Thorpe et al., 2007) and chimpanzees use it in both arboreal and terrestrial contexts for foraging and during investigations (Pernell et al., 2021; Drummond-Clarke et al., 2022; Hunt, 1994).

In the context of baboon locomotor development, it appears that infant baboons develop bipedal walking skills very early. Neuromotor development through quadrupedal experience contributes to their ability to walk bipedally for few steps from 5 months old (Druelle et al., 2017). At 1.5 years old

they can spontaneously walk bipedally for longer periods, as adults do. However, at this age, and although their coordination and rhythmicity are improved, the kinematic strategy remains distinct from mature individuals, resulting in significantly higher costs for bipedal walking, albeit with low differences in absolute values.

Baboons versus humans

According to our results on the minimal cost of transport, baboons could theoretically expend the same amount of energy as humans to walk bipedally if an effective energy transfer mechanism was present. However, energy recovery is substantially lower in baboons compared to humans (~53-68% in Ortega, & Farley, 2005; 23-74% in humans in the present study based on Lencioni et al., 2019). When comparing adult baboons walking bipedally with a flexed posture to adult humans walking bipedally with an extended posture, some similarities in energy transfer patterns emerge, specifically in the hindlimb. The transfer of energy in the thigh and the shank of baboons is not significantly different from what is observed in humans. The movement of the thigh follows a passive pendulum mechanism during occasional bipedal walking in baboons. On the other hand, the shank as a segment relies more on in-phase fluctuations of potential and kinetic energies, suggesting that if elastic properties are present and can be efficiently used, energy could be stored and released in this segment during this mode (Aerts et al., 2018). For instance, humans rely on a well-developed Achilles tendon, which enables them to efficiently store and release energy during locomotion (e.g., Butler, & Dominy, 2016; Bramble, & Lieberman, 2004; Blazeovich, & Fletcher, 2023; Kharazi et al., 2021). Baboons also possess a developed Achilles tendon, yet it is not exactly organized like humans and it is not known how much they can rely on it to store and release energy.

Important differences are evident in the movement of the foot, trunk and arm segments. The foot of baboons is semiplantigrade, working in a manner distinct from that of humans (Berillon et al., 2010) and early hominins (Prang, 2023). Furthermore, the movement of the trunk differs fundamentally; in humans it ascends and descends during the stride cycle, thus resembling the inverted pendulum motion of the body centre of mass. In humans, the virtual limb connecting the body centre of mass to the foot aligns with the anatomical limb connecting the pelvis to the foot (see Druelle et al., 2023), giving rise to this particular movement pattern of the trunk centre of mass (Figure 4 a,c). In contrast, baboons, adopting a “bent-hip, bent-knee” posture, experience a shift of the virtual limb in front of the anatomical limb, resulting in strong trunk stabilization and minimal fluctuations in potential energy (Figure 4 b,d). Nevertheless, our results indicate that subtle adjustments in trunk movement could significantly enhance the rate of energy recovery of the BCoM in baboons. Regarding arm movement, the stability observed in baboons (Berillon et al., 2010) clearly restricts energy recovery potential,

contrasting with the clear efficiency observed in human bipedal locomotion. In humans, arm movement is mostly a passive mechanism that counterbalances the angular momentum of the lower limbs, thus serving to reduce energy expenditure (De Graaf et al., 2019; Pontzer, Raichlen, & Sockol, 2009; Meyns, Bruijn, & Duysens, 2013).

A possible route toward bipedal improvement during hominin evolution

The way animals move around is subject to strong selective pressures favouring efficiency (Reilly et al., 2007). Efficiency is thought to have been an important factor for early hominins as bipedalism became a more frequent part of their locomotor repertoire (Rose, 1991; Senut et al., 2001; White, Lovejoy, Asfaw, Carlson, & Suwa, 2015; Almécija et al., 2021; Daver et al., 2022). Over generations, the increasing reliance on bipedalism should be correlated with fitness factors such as juvenile survivorship and mating success. Evidence from fossil discoveries and comparative anatomical studies indicates that bipedalism may have evolved to minimize energetic costs (Bramble, & Lieberman, 2004; Pontzer, 2017). Comparative analyses of the anatomies of extinct and extant primates support a gradual refinement through natural selection (e.g., Almécija et al., 2013; Daver et al., 2022). Furthermore, there are now multiple studies suggesting that australopithecines possessed skeletal adaptations related to improved efficiency of bipedal walking (Ohman, Krochta, Lovejoy, Mensforth, & Latimer, 1997; Sellers, Cain, Wang, & Crompton, 2005; Ward, Kimbel, & Johanson, 2011; Vidal-Cordasco et al., 2017; McNutt, & DeSilva, 2020), and that their bipedal behaviors were most probably performed with an erect and extended posture (Crompton et al., 1998; Wang, Crompton, Li, & Gunther, 2003; Nagano et al., 2005; DeSilva et al., 2013; Foster, Raichlen, & Pontzer, 2013; Ward, 2013; Wiseman, 2023). However, the bipedal posture (flexed or extended) of earlier hominins such as *Ardipithecus ramidus*, *Orrorin tugenensis*, and *Sahelanthropus tchadensis* remains unknown so far, mainly because of the fragmentary nature of the fossil remains. As a result, comparing non-human primate models, which exhibit a flexed posture, with human walking, characterized by an extended posture, can provide valuable information. Specifically, analysing energy conservation and exchange during bipedal walking in non-human primates can help discern which body segments may have been subject to strong selective pressures during the evolution of bipedalism. This approach provides an experimental and mechanical framework to formulate new hypotheses based on extant models, and compare them with those derived from fossil discoveries (e.g., Oku, Ide, & Ogihara, 2021; O'Neill et al., 2022; Druelle et al., 2024). While baboon morphology differs significantly from early hominins, studying it within this framework illustrates how a “non-human primate morphology” can adjust to walk bipedally, despite retaining the flexed posture seen in other non-human primates, and potentially in early hominins.

Reconciling the current results with the fossil record

It is widely accepted that Miocene apes and hominins did not exhibit a complete set of morphological traits conducive to sustainable bipedal behaviors (see Almécija et al., 2021 for a review). Considering that flexed posture characterizes the bipedal locomotion of non-human primates, bipedal locomotion with flexed postures and low rates of energy recovery likely constituted an early stage in the evolution of bipedalism. In such a theoretical framework, our current findings would suggest that a gradual transition towards improved trunk motion may have been accompanied by a significant shift in total energy recovery. As a result, a flexed posture, albeit energetically demanding, might have persisted while trunk movement was refined during bipedal ambulation. *Ardipithecus ramidus* (~4.4 Mya) emerges as a potential fossil hominin fitting this evolutionary scenario, given notable anatomical changes observed in the pelvic bone (Lovejoy, Suwa, Spurlock, Asfaw, & White, 2009; White et al., 2015). The upper pelvis exhibits a broader and more sagittally facing iliac blade compared to extant non-human catarrhines, a reduced distance between the sacroiliac articulation and hip joint, the presence of the anterior inferior iliac spine, and a pronounced sciatic notch (Lovejoy et al., 2009). All together, these traits could change the lever arms of muscles such as the gluteus medius that helps support the trunk on the hindlimbs during the stance phase. As a result, these traits might be functionally relevant for maintaining a more upright bipedal posture and stabilizing the trunk. Despite the persistence of a long lower pelvis and a grasping foot, these traits point to initial pelvic adaptations related to a form of bipedal behavior present in its repertoire (White et al., 2015). The results of our study align with the observed evolutionary patterns in fossil remains of early hominins, in the sense that the enhancement of bipedal movement may have involved early gradual anatomical changes in the pelvis. In other words, subtle refinements in bipedal movement, as the ones observed in our study, could have substantially increased the energetic recovery rate, making it relevant for regular use, especially in conjunction with demanding locomotor modes like vertical climbing and arboreal quadrupedalism (e.g., Hanna, Schmitt, & Griffin, 2008; Schmitt, 1999).

Data availability statement

The complete baboon dataset from the current study is accessible through the following link on the Open Science Framework (OSF) website:

https://osf.io/6jxb4/?view_only=27bbd19e1ed54722bad0f29302bfb616

If you encounter any issues when trying to access the dataset, please reach out to the study's corresponding author for assistance.

Acknowledgments

We are very grateful to Guy Dubreuil and Romain Lacoste, successive directors of the Primatology Station of the CNRS at the time the data were collected, who provided access and facilities to the

animals. We are very grateful to Christophe Arnoult and Alexia Cermolacce, the current director and the operational director, respectively, of the Primatology Station of the CNRS, for their continuous support. The Technical Platform has been initially funded by the CNRS-INEE. This project was also funded by ANR-18-CE27-0010-01 and CNRS-INEE International Research Network IRN-GDRI0870.

Author contribution statement

François Druelle: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (lead); methodology (lead); project administration (equal); resources (equal); software (lead); supervision (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Jonathan Özçelebi:** Data curation (equal); Formal analysis (equal); Investigation (equal); resources (equal); writing – review and editing (equal). **François Marchal:** Conceptualization (equal); data curation (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (equal); resources (supporting); supervision (equal); validation (supporting); writing – review and editing (equal). **Gilles Berillon:** Conceptualization (equal); data curation (lead); formal analysis (supporting); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (leads); software (equal); supervision (equal); validation (equal); writing – review and editing (equal).

Conflict of interest

Authors declare no competing interests.

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Figures

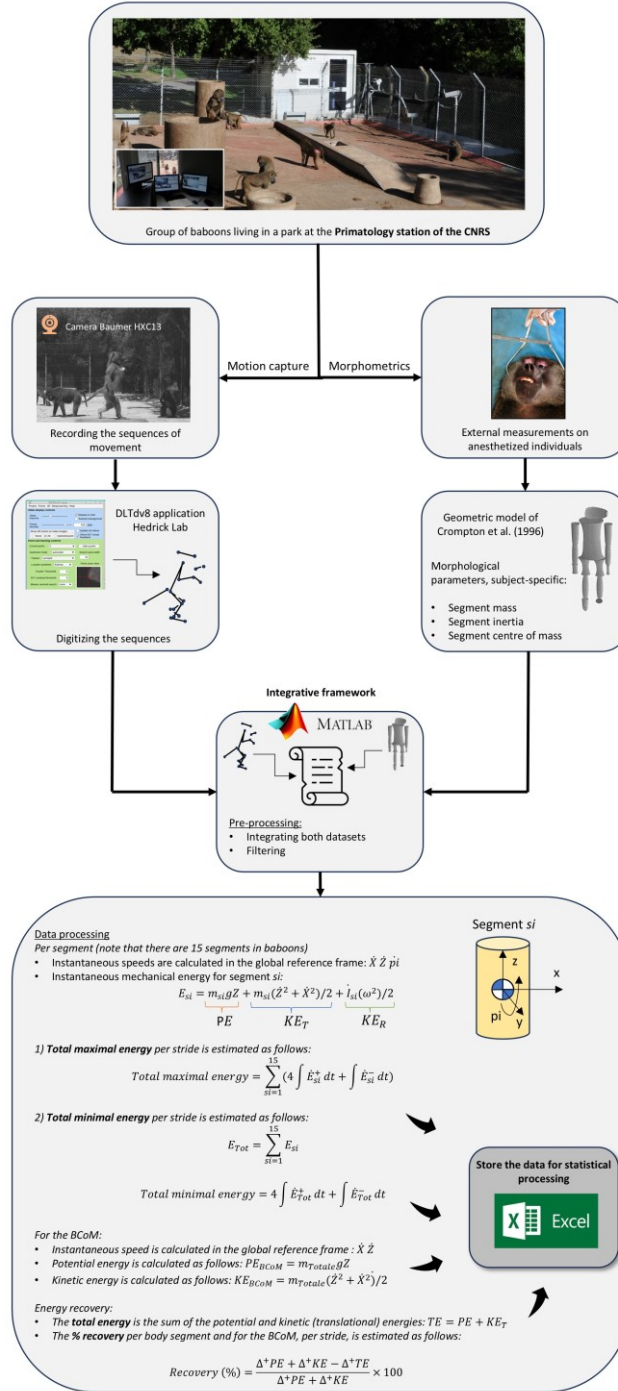


Figure 1. Workflow of the present study. The kinematic data are from Druelle et al. (2022) and the morphometrics data are from Druelle et al. (2017). In the calculation of the total maximal energy, the instantaneous energy (E_{si}) and the instantaneous power is calculated for each segment (\dot{E}_{si}). Then, a) the time integral of all \dot{E}_{si}^+ is multiplied by 4 (given the 25% efficiency for the conversion of chemical energy into positive mechanical work); b) the time integral of all \dot{E}_{si}^- is multiplied by 1 (given the 100% efficiency for negative power). Finally, the total maximal energy is obtained by summing components a) and b). In the calculation of the total minimal energy, the total energy (E_{tot}) is calculated by summing all E_{si} values and the total instantaneous power is calculated (\dot{E}_{tot}). The total minimal energy is obtained by summing the time integral of $\dot{E}_{tot}^+ \times 4$ and the time integral of \dot{E}_{tot}^- .

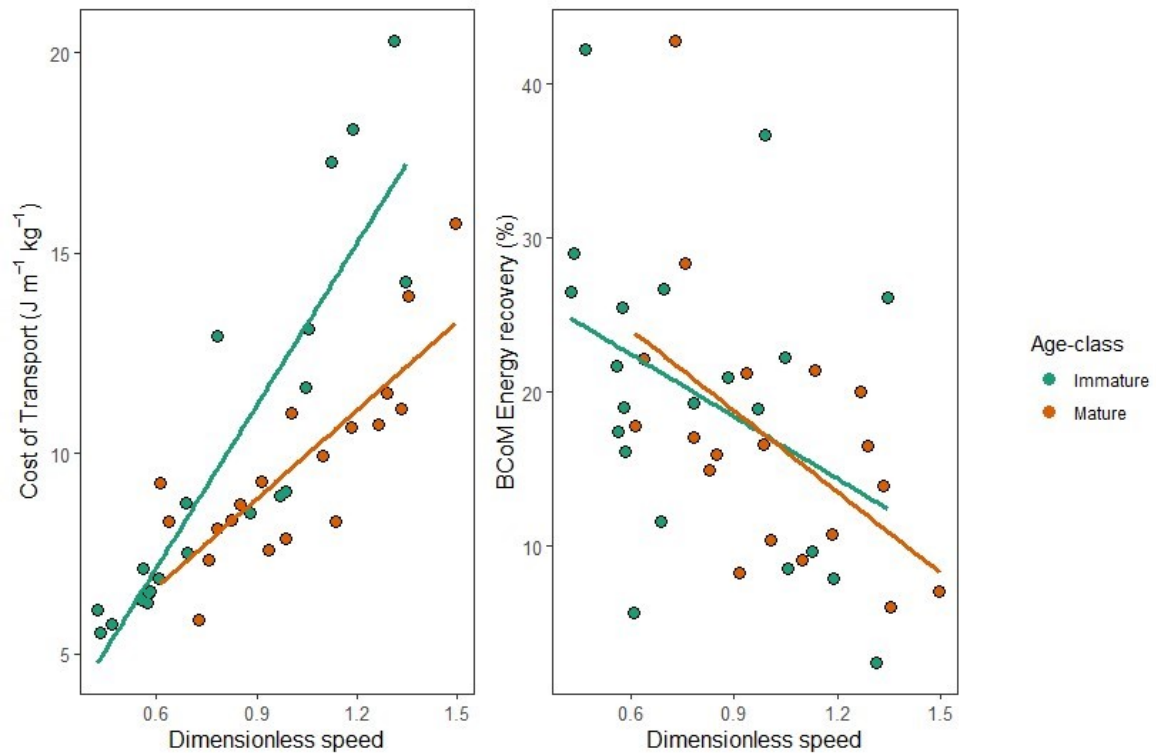


Figure 2. Influence of the speed of progression on the maximal cost of transport and the energy recovery rate during occasional bipedal walking. There is a significant positive relationship between speed and the maximal cost of transport (left panel) in immature (green) and mature (orange) individuals, but in immature individuals there is a stronger positive relationship than in mature individuals. There is a significant negative relationship between speed and the energy recovery rate in both immature and mature individuals. There is no difference between age-classes.

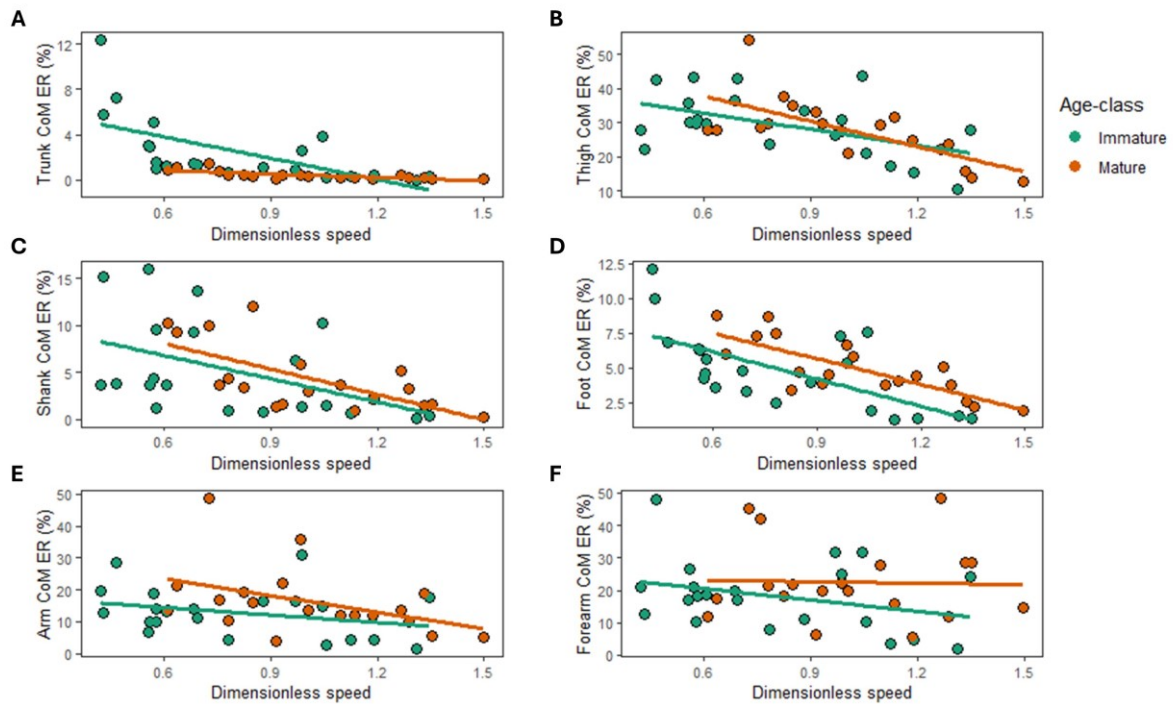


Figure 3. Influence of the speed of progression on the energy recovery rate of the trunk, thigh, shank, foot, arm and forearm during occasional bipedal walking. There is a general significant negative relationship between speed and the energy recovery rate of the trunk (A), and immature individuals have a higher energy recovery rate in the trunk than mature individuals. There is a general significant negative relationship between speed and the energy recovery rate of the shank (C), and immature individuals have a higher energy recovery rate in the shank than mature individuals. There is a general significant negative relationship between speed and the energy recovery rate of the thigh (B), foot (D), arm (E), and forearm (F), and for these segments there is generally no difference between age-classes.

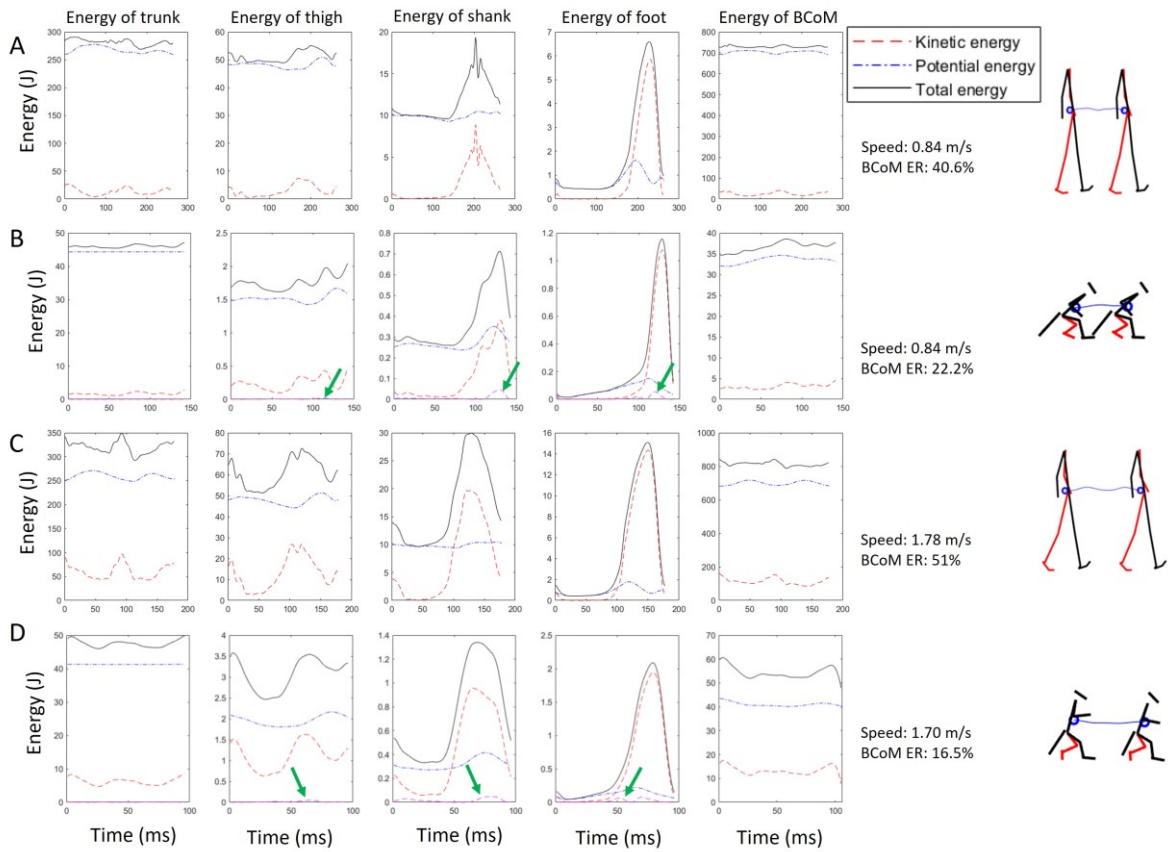


Figure 4. Examples of the variation in kinetic, potential and total energy at two different speeds of progression in humans and baboons for the trunk, thigh, shank, foot, and BCoM. Minimum values of the comparative speed range are provided in a human (A) and a baboon (B), and maximum values are provided in a human (C) and a baboon (D). The green arrows indicate the curve of the rotational kinetic energy in baboons.

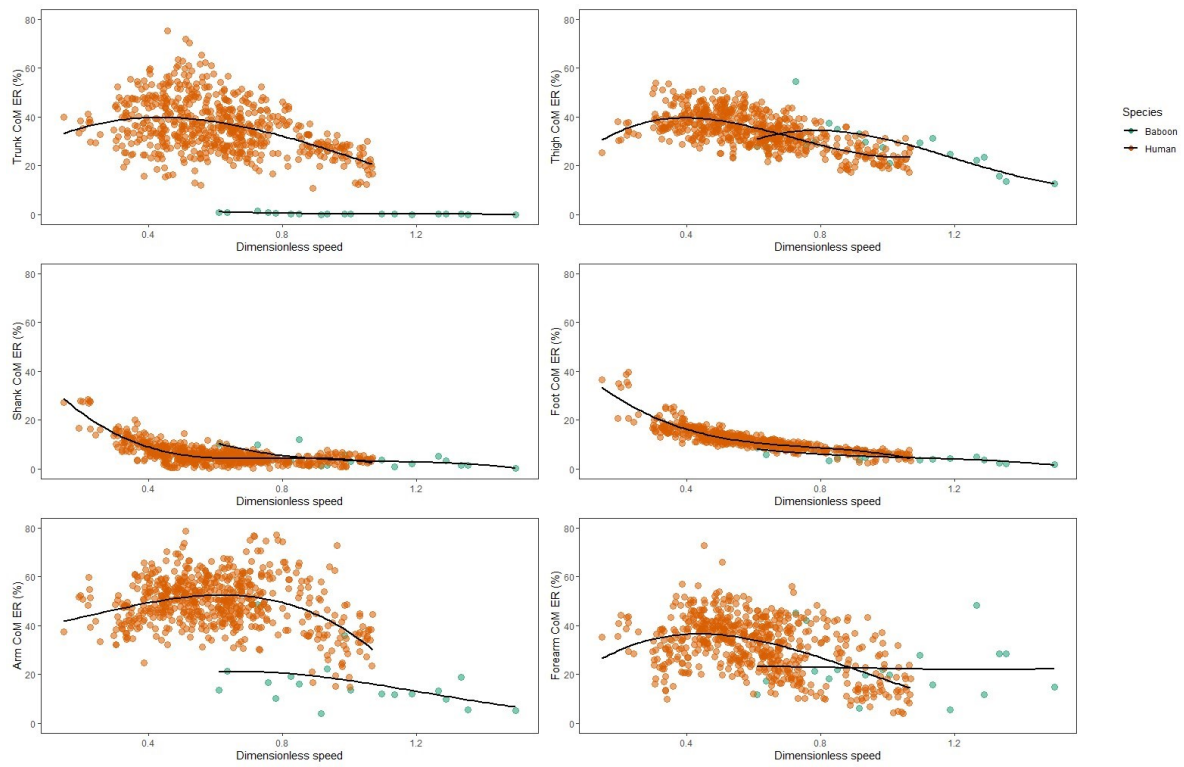


Figure 5. Relationships between the dimensionless speed and energy recovery within the different body segment studied in baboons and humans, i.e., the trunk, the thigh, the shank, the foot, the arm and the forearm.

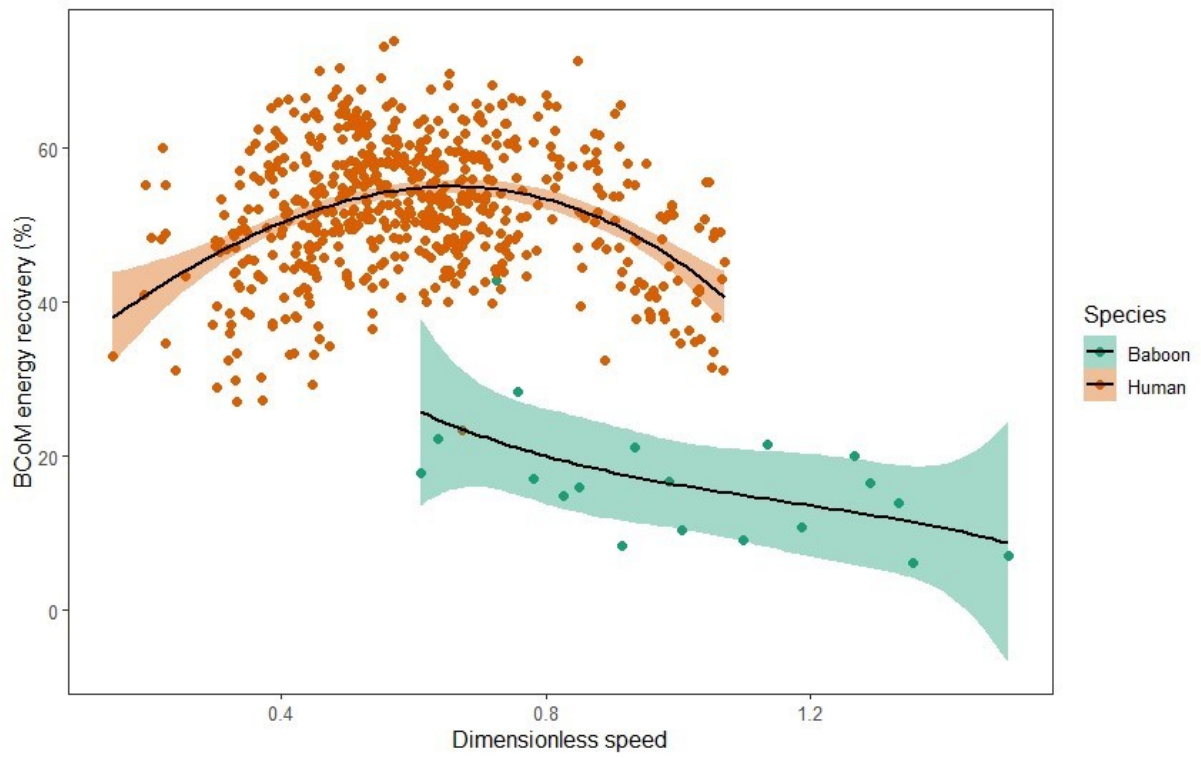


Figure 6. Relationship between the dimensionless speed and energy recovery of the BCoM in humans and baboons. The shaded area represents the 95% confidence interval for each sample.