

# Chimpanzee Locomotor Energetics and the Origin of Human Bipedalism

SOCIAL SCIENCE: Anthropology

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## Abbreviations

$V_{\text{musc}}$  Volume of muscle ( $\text{cm}^3$ ) activated per unit ground force during locomotion  
 $t_c$  Contact time (s); the duration of foot-ground contact for one step  
COL The energy cost of locomotion, measured as the mass-specific rate of oxygen consumption ( $\text{mlO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ )

**Abstract:**

Bipedal walking is evident in the earliest hominins (1), but why our unique two-legged gait evolved remains unknown. Here, we analyze walking energetics and biomechanics for adult chimpanzees and humans to investigate the long-standing hypothesis that bipedalism reduced the energy cost of walking compared to our ape-like ancestors (2). We find that human walking is 75% less costly than chimpanzee walking due to our more extended hip and a longer hindlimb, features present in early fossil hominins. Analyses of bipedal walking in chimpanzees indicate that bipedalism in early, ape-like hominins could indeed have been less costly than quadrupedal knucklewalking.

**Text:**

As predicted by Darwin (3), bipedalism is the defining feature of the earliest hominins (1), and thus marks a critical divergence of the human lineage from the other apes. One enduring hypothesis is that bipedalism evolved to reduce locomotor costs in early hominins, relative to the ape-like Last Common Ancestor (LCA) of chimpanzees and humans (2). Testing this hypothesis requires comparative data on not only the cost of locomotion in humans and chimpanzees, but also on the biomechanical determinants of these costs. However, the only previous study of chimpanzee locomotor cost used juvenile chimpanzees and indicated that bipedalism and quadrupedalism were equally costly in chimpanzees, and both were more costly than human locomotion (4). While this study has been central to the debate over energetics and the evolution of bipedalism (2,5), the reliability of these data has been questioned because adult and juvenile locomotor mechanics and costs can differ substantially (5), and because of recent evidence that bipedalism is more costly than quadrupedalism in other primates (6). Further, Taylor and Rowntree's (4) study did not include a biomechanical analysis of the determinants of chimpanzee locomotor costs, limiting the potential application of the study to the hominin fossil record.

Here, we compare human and adult chimpanzee locomotor energetics and biomechanics in order to determine links between anatomy, gait and cost. We focused on walking speeds, since walking is the gait commonly used during terrestrial travel in wild chimpanzees (7). We tested two sets of predictions; first, based on recent studies of primate mechanics and energetics (6,8), we predicted that bipedal and quadrupedal (i.e.,

“knucklewalking”) costs will differ in adult chimpanzees, and that both bipedal and quadrupedal walking in chimpanzees will be energetically more costly relative to other quadrupeds and humans. Second, following previous work (9,10), we predicted that these differences in cost would be explained by corresponding differences in 1) the force required to support bodyweight during each step, and 2) the volume of muscle activated to generate one unit of ground force. Accordingly, we collected metabolic, kinematic and kinetic data during walking from 5 chimpanzees, aged 6 – 33 years, and 4 adult humans (see Table 1 and Methods). The magnitude of ground force was estimated as the inverse of the duration of foot-ground *contact time*,  $t_c$ , per step (9,11), while the volume of muscle activated per unit of ground force,  $V_{\text{musc}}$ , was estimated using inverse dynamics (12) (see Methods). Following Roberts et al. (10), we predicted that the cost of locomotion, COL ( $\text{mlO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ ) varies as the ratio of active muscle volume and contact time,  $V_{\text{musc}}/t_c$ . Thus, any difference in  $V_{\text{musc}}/t_c$ , either between species or gaits, should lead to a proportional difference in COL. Using this approach allowed us to link differences in anatomy and gait to cost in order to establish what changes – if any – would lower the cost of bipedalism for a chimpanzee-like early hominin, such that bipedalism would be more economical than the ape-like quadrupedalism of the human-chimpanzee LCA.

The mass-specific cost of transport ( $\text{mlO}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ) for chimpanzees was greater than expected for their body size (13) (Fig. 1). By contrast, human walking was less expensive than expected for their body size, and substantially (~75%) less expensive than chimpanzee locomotion (Fig. 1). Within the entire chimpanzee sample, bipedal walking

was modestly, but not significantly, more costly (~10%) than quadrupedal walking (Fig. 1). However, differences in bipedal and quadrupedal cost varied among individuals (Fig. 1), and in contrast to Taylor and Rowntree (4), most subjects exhibited significant differences between gaits. For three chimpanzees (C1 – C3) bipedalism was 32.2% more expensive ( $p < 0.001$ , Student's paired t-test), but for two other chimpanzees, bipedal costs were similar ( $p = 0.39$ , C5) or even less than quadrupedal costs ( $p < 0.05$ , C4).

As predicted, differences in kinematics and estimated muscle activation explained observed differences in cost between bipedal and quadrupedal walking, and between humans and chimpanzees. In the three chimpanzees for which active muscle volumes were estimated (subjects C1 – C3, see Methods), an increase in active muscle volume and shorter contact times increased  $V_{\text{muscle}}/t_c$  by 35.2% ( $\pm 5.2\%$ ) during bipedal walking compared to quadrupedal walking. This difference corresponds closely to the observed 32.2% ( $\pm 3.2\%$ ) increase in COL during bipedal walking for these subjects (Fig. 2, 3). When human walking was compared to chimpanzee bipedal walking, humans activated smaller muscle volumes per unit body mass, and employed longer contact times than bipedal chimpanzees (Fig. 2). These differences caused a 79.4% ( $\pm 1.6\%$ ) lower ratio of  $V_{\text{muscle}}/t_c$ , which corresponded closely to the observed 76.8% ( $\pm 2.6\%$ ) decrease in locomotor cost (Fig. 3). Similarly, although contact times for quadrupedal chimpanzees were slightly longer than for humans, they activated so much more muscle that  $V_{\text{muscle}}/t_c$  was 72.8% ( $\pm 4.6\%$ ) lower for humans than for quadrupedal chimpanzees, matching the 68.5% ( $\pm 4.3\%$ ) difference in COL (Fig. 2, 3).

Interspecific differences in contact time and active muscle volume point directly to anatomical and kinematic sources for the observed differences in cost between chimpanzees and humans. First, the shorter legs of chimpanzees (Table 1) lead to shorter contact times for a given speed (e.g., see Hoyt et al. (14)) during bipedal walking (Fig. 2C), which increases the magnitude of the ground reaction force (GRF) impulse for each step. That is, due to their shorter hindlimbs, bipedal chimpanzees must generate greater ground forces at a faster rate than humans, thereby increasing bipedal costs (9,11). Conversely, the long forelimbs of chimpanzees increase contact times, and decrease ground force impulses, during quadrupedal walking. Second, the bent-hip, bent-knee gait of chimpanzees positions the body's center of mass anterior to the hip joint and increases the moment arm of the GRF. This posture generates large external flexion moments (Fig. 2A) that, when combined with chimpanzees' long muscle fibers (15), must be opposed by activating a correspondingly large volume of hip extensor muscle (Fig. 2B). Additionally, the long muscle fibers (15) and crouched posture of chimpanzees result in large active muscle volumes at the knee (Fig. 2B). In contrast, humans decrease active muscle volume by adopting an upright posture, which orients the GRF vector nearer to the hip and knee joints and confines large moments to the ankle where muscle fibers are short (Fig. 2A). Thus, even though the long forelimbs of chimpanzees enable them to knucklewalk using longer contact times than humans at dynamically similar speeds (Froude number  $\sim 0.2$ ), walking costs are lower in humans than in chimpanzees.

The influence of contact time and joint angle on locomotor cost is further supported by subject C4. Only this chimpanzee used longer contact times during bipedal

walking, and flexed her knee and hip to a similar degree during bipedal and quadrupedal walking (Fig. 4). As expected, C4 was also the only subject whose costs were lower during bipedal versus quadrupedal walking, although not as low as in humans (Fig. 1). These results highlight how slight kinematic changes can lead to large variations in locomotor cost, and are consistent with previous work demonstrating that differences in posture can affect cost (16-18). Note however, that chimpanzees cannot employ the full hip and knee extension typical of humans because of their distally oriented ischia, which reduce the hamstrings' ability to produce an extensor moment when the femur is extended relative to the pelvis (19,20). Chimpanzee pelvic anatomy thus requires them to walk with a flexed hip and knee throughout their stride. In contrast, human ischia are oriented dorsally, allowing large hamstrings extensor moments when the femur is fully extended (19).

Our results generate two testable predictions for the hominin fossil record. If locomotor economy was a selective force behind hominin bipedalism, then early hominin lower limbs should be longer than those of apes, and the ischia of early hominin pelvises should be more dorsally projecting. The fossil record does not yet allow us to test these predictions in the earliest hominins, but an increase in leg length is apparent in partially complete specimens of *Australopithecus afarensis* (AL-288) and *A. africanus* (21,22), consistent with selection to increase contact times, and thereby lower locomotor cost. Further, *A. afarensis* (AL 288-1) and *A. africanus* (STS-14) both have a more dorsally oriented ischium compared to chimpanzees (19,20,23). These modifications would have increased the mechanical advantage of the hamstrings when the hip was fully extended,

greatly reducing active muscle volume and thus lowering walking costs. Notably, our results suggest that even early transitional forms would have reaped some energy savings with minor increases in hip extension and leg length. Indeed, given the evidence that the LCA of humans and chimpanzees was a chimpanzee-like knucklewalker (24), the variation within our chimpanzee sample (Fig. 4) demonstrates that some members of the LCA population likely had the ability to extend their hindlimb more fully and to use longer contact times during bipedal locomotion. This would have decreased the cost of bipedal walking below that of quadrupedal knucklewalking in these individuals (Fig. 4, Table 1). Thus, our results support the hypothesis that energetics played an important role in the evolution of bipedalism. Future fossil discoveries from the earliest hominins will resolve whether this energetic advantage was the key factor in the evolution of hominin bipedalism.

## **Methods**

Five chimpanzees (2 males, 3 females; mean age 18.2 yrs, range 6 – 33) were trained over the course of 14 months to walk quadrupedally (i.e., knucklewalk) and bipedally on a treadmill (Smooth Fitness 9.15, Sparks, NV). Three of these subjects (C1 – C3) were also trained to walk down a force-plate equipped track. All subjects are socially housed in large, outdoor enclosures at a USDA registered and approved facility. IACUC approval was obtained prior to the beginning of the study, and institutional animal care guidelines were followed throughout.



During treadmill trials, subjects wore loose-fitting masks that collected expired air, and the mass-specific cost of locomotion, COL ( $\text{mlO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ ), was measured via established open-flow methods (13). COL was measured at a range of speeds for each individual. Only trials lasting a minimum of three minutes, and in which oxygen-consumption rate visibly plateaued, were included for analysis. Multiple COL measurements were taken at each speed for each subject, and means used for subsequent analyses. For a sub-set of treadmill trials, a set of kinematic variables, including contact time,  $t_c$  (i.e., duration of stance for one foot or hand) was collected via high-speed video (Redlake, 125fps).

During force-plate trials, subjects walked down a 10-meter track equipped with an embedded force-plate (Kistler) recording at 4 kHz, providing vertical and fore-aft ground reaction forces, GRF. Simultaneous kinematic data were collected via high-speed video (Redlake, 125fps), with joint centers for front- and hind-limbs (shoulder, elbow, wrist, hip, knee, ankle) marked on each subject using non-toxic water-based white paint. Because flexion and extension of the limb joints occurs primarily in the sagittal plane during walking, and since mediolateral forces were smaller than antero-posterior ground forces and generally less than 10% of vertical ground forces, we restricted our analyses to the sagittal plane. Force-plate trials were accepted only if one limb (fore or hind) contacted the force-plate cleanly, and if fore-aft GRF traces indicated constant forward speed.

Body mass and external measurements for each subject were used to calculate segment inertial properties following Raichlen (25). Inverse dynamics were then used to

calculate joint moments after Winter (12), using force and kinematic data. Joint moments were combined with published data on chimpanzee muscle moment arms (15) in order to calculate the opposing extensor muscle forces generated for each muscle group. The volume of muscle activated for each step was then calculated following Roberts et al. (10), using published muscle fiber lengths (15).

Previous work (10) has shown that the mass-specific energy cost of locomotion, COL ( $\text{mlO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ ) for terrestrial animals is a function of contact time,  $t_c$ , and the volume of muscle,  $V_{\text{musc}}$  ( $\text{cm}^3 \text{ N}^{-1}$ ), activated to apply a unit of ground force, such that:

$$\text{COL} = k \frac{V_{\text{musc}}}{t_c} \quad (1)$$

where  $k$  is a constant relating oxygen consumption and force production ( $\text{mlO}_2 \text{ N}^{-1}$ ). This relationship holds because the energy cost of locomotion derives primarily from muscle forces generated to support bodyweight.

For comparison with humans, a similar dataset of locomotor cost, kinematics, and muscle activation was collected for a sample of four humans (1 female, 3 males). Subjects were recreationally fit adults with no gait abnormalities, and gave informed consent for this study. Human subjects committee approval was obtained prior to this study, and institutional guidelines were followed throughout. Methods for obtaining locomotor cost and kinetic data were identical to those used for chimpanzees, with the following exceptions: kinematics were measured via a high-speed infrared motion analysis system (Qualisys®), data for muscle fiber lengths and joint mechanical

advantage were calculated following Biewener et al. (18), and segment inertial properties were calculated following Winter (12).

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**Table 1.** Chimpanzee and human costs of transport. Individual means (standard errors) calculated from 4 speeds in each gait for each subject. Species means calculated from individual means. Froude number calculated from hip height following Alexander and Jayes (26). *P*-values are 1-tailed, for paired-samples Student's *t*-tests.

Subject	Mass (kg)	Hip			Cost of Transport ( $\text{mlO}_2 \text{ kg}^{-1} \text{ m}^{-1}$ )			<i>p</i>
		Height (cm)	Speed (m/s)	Froude Number	Bipedal	Quadrupedal		
C1 (6yr ♂)	33.9	45.0	1.0	0.2	0.28 (0.033)	0.18 (0.012)	0.03	
C2 (9yr ♂)	51.6	52.5	1.0	0.2	0.26 (0.017)	0.18 (0.007)	0.01	
C3 (19yr ♀)	63.9	51.0	1.0	0.2	0.20 (0.011)	0.14 (0.014)	0.02	
C4 (33yr ♀)	67.3	41.3	1.0	0.2	0.16 (0.020)	0.29 (0.021)	0.02	
C5 (27yr ♀)	82.3	40.5	1.0	0.3	0.15 (0.011)	0.16 (0.006)	0.39	
Chimpanzees (n=5)	59.8	46.1	1.0	0.2	0.21 (0.014)	0.19 (0.013)	0.16	
Humans (n=4)	69.3	92.2	1.3	0.2	0.05 (0.004)			

## Figure Legends

**Figure 1.** Net cost of transport ( $\text{mlO}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ) for chimpanzee quadrupedal walking (blue), chimpanzee bipedal walking (red), and human walking (yellow). Dashed lines indicate trendlines for running and walking in birds and mammals. Running trendline from Taylor et al.<sup>13</sup>. Walking data collected from the literature (see Supplemental Data, Table S1); open symbols indicate individual species.

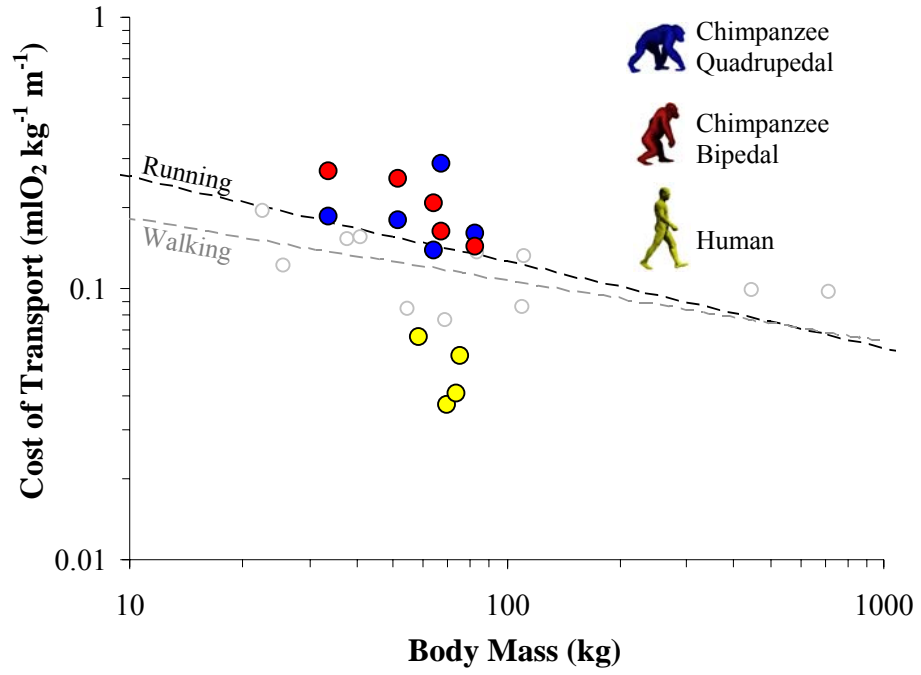
**Figure 2. A.** GRF vectors and joint torque for humans and chimpanzees. Figures show joint positions at 50% stance (forelimb and hindlimb shown separately for quadrupedal chimpanzees). Positive torque values indicate flexion, negative values indicate extension. Note the large hip flexion moments in chimpanzees relative to humans. **B.** Active muscle volume per Newton of bodyweight ( $\text{cm}^3/\text{N}$ ) at each joint and in the whole limb for chimpanzee hindlimbs (dark blue) and forelimbs (light blue) during quadrupedal walking, chimpanzee hindlimbs during bipedalism (red), and human hindlimbs (yellow). **C.** Mean contact time,  $t_c$  (s), during walking in chimpanzees and humans. Note that Froude numbers are similar for all groups ( $\text{Fr} = 0.2$ , Table 1), but absolute speeds are slightly higher for humans (Table 1).

**Figure 3.** Comparison of differences in the ratio of active muscle volume to contact time,  $V_{\text{muscle}}/t_c$  (white bars) and the cost of locomotion, COL ( $\text{mlO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ , gray bars), between gaits and species. Error bars indicate  $\pm$  one standard error of the mean percent difference.

**Figure 4.** Comparison of thigh angle, knee flexion, and contact time for C4 versus other chimpanzees (n=4). Thigh angles measured as angle between the thigh segment and the horizontal (e.g. thigh angle is 90 degrees when the thigh is perpendicular to the ground). Knee angle measured as the angle between the thigh and leg where full knee extension is 180 degrees. Contact time is the time elapsed from touchdown to toe-off. Asterisks (\*) indicate significant differences between quadrupedal (blue) and bipedal (red) and strides ( $p < 0.05$ , Student's paired t-test).



Figure 1



**Figure 2**

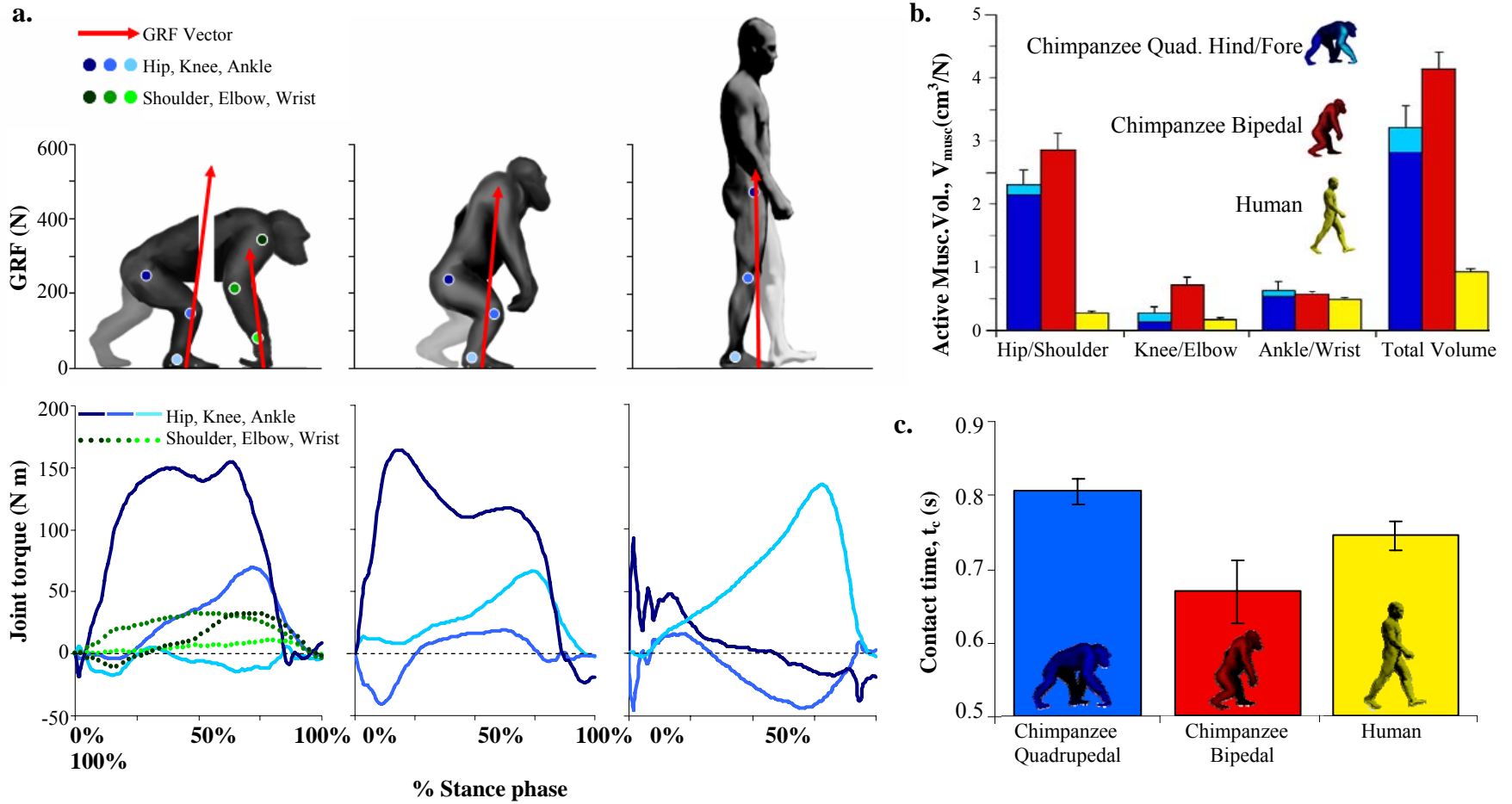
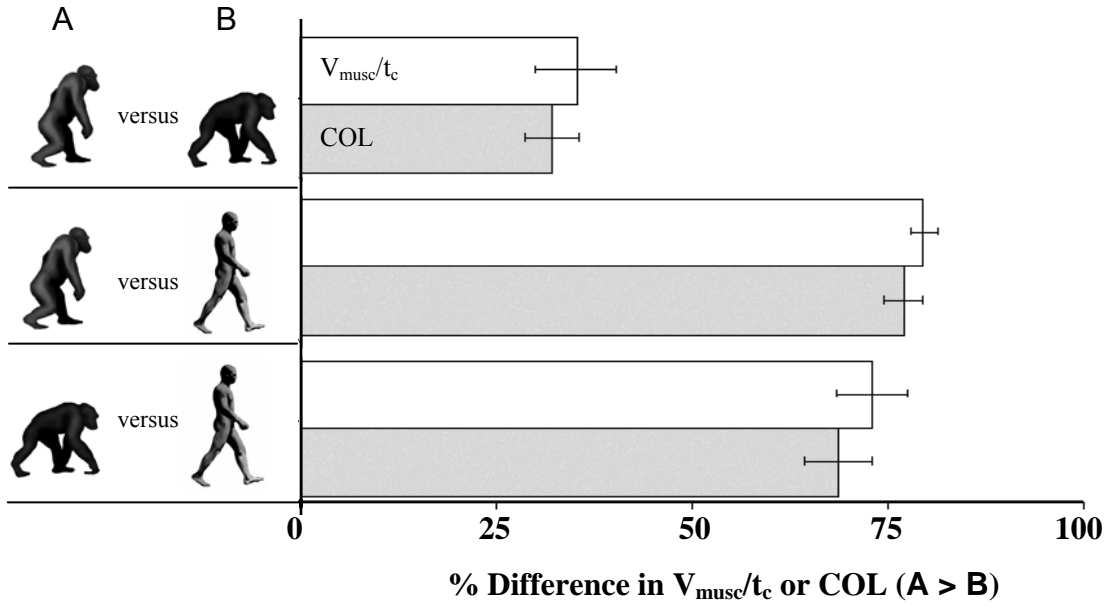
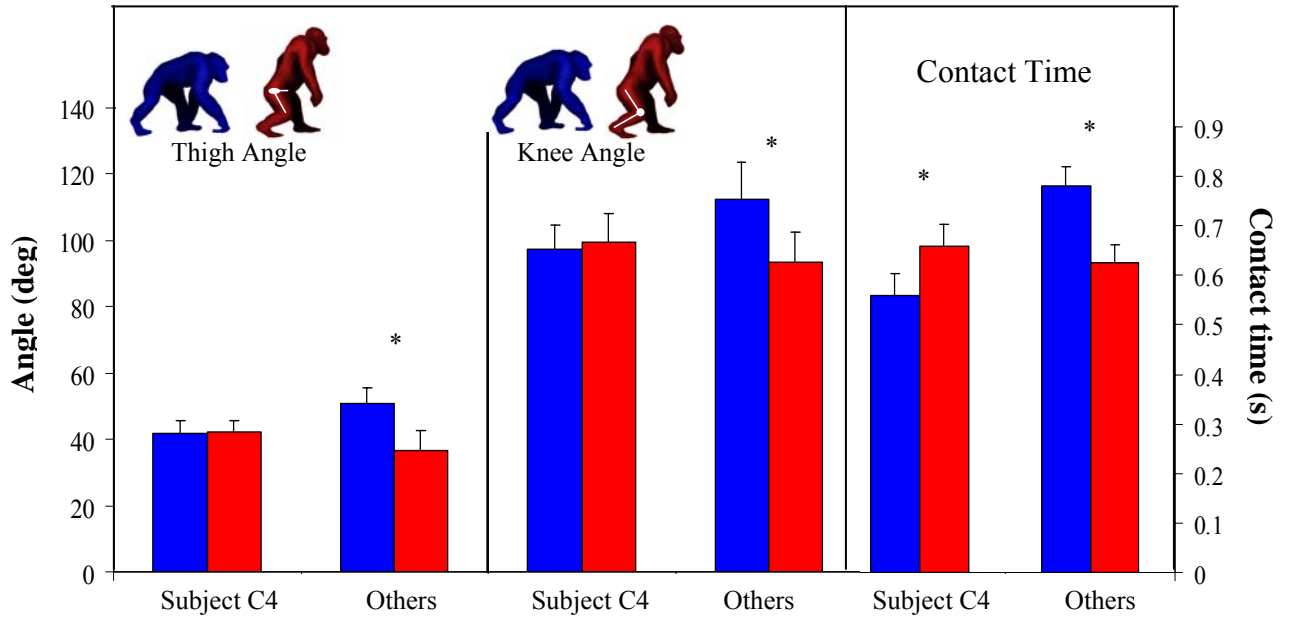


Figure 3.



**Figure 4.**



## Supporting Online Material:

**Table S1.** The cost of transport, COT (mlO<sub>2</sub> kg<sup>-1</sup> m<sup>-1</sup>), during walking for a sample of terrestrial animals.

Species	Mass (kg)	COT	Source
Dog ( <i>Canis familiaris</i> )	38	0.15	Pontzer (2007)
Caribou ( <i>Rangifer tarandus</i> )	25.5	0.12	Luick and White (1986)
Caribou ( <i>Rangifer tarandus</i> )	54.5	0.08	Luick and White (1986)
Caribou ( <i>Rangifer tarandus</i> )	110	0.09	Fancy and White (1986)
Goats ( <i>Capra hircus</i> )	22.65	0.19	Pontzer (2007)
Elephants ( <i>Loxodonta africana</i> )	1542	0.04	Langman et al. (1995)
Horse: Miniature ( <i>Equus caballus</i> )	112	0.13	Griffin et al. (2004)
Horse: Arabic ( <i>Equus caballus</i> )	448	0.1	Griffin et al. (2004)
Horse: Draft ( <i>Equus caballus</i> )	715	0.1	Griffin et al. (2004)
Ostrich ( <i>Struthio camelus</i> )	68.5	0.08	Rubenson et al. (2004)
Iberian pigs ( <i>Sus mediterraneus</i> )	41.3	0.15	Lachica and Aguilera (2000)
Iberian pigs ( <i>Sus mediterraneus</i> )	84.1	0.14	Lachica and Aguilera (2000)
Platypus ( <i>Ornithorhynchus anatinus</i> )	1.4	0.28	Fish et al. (2001); Berthge et al. (2001)

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