Evolution of Hominin Forelimbs in the Context of Bipedalism

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Evolution of Hominin Forelimbs in the Context of Bipedalism

A dissertation presented

by

Andrew Kevork Yegian

To

The Department of Human Evolutionary Biology

In partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

in the subject of

Human Evolutionary Biology

Harvard University

Cambridge, Massachusetts

May, 2019
Evolution of Hominin Forelimbs in the Context of Bipedalism

Abstract

The evolution of bipedalism in the hominin lineage coincided with a major shift in the locomotion function of the forelimbs, from producing external forces in contact with the substrate in the arboreal and quadrupedal last common ancestor with chimpanzees, to producing no external forces but swinging as angular momentum counterweights to the legs in striding bipedalism. The shift in forelimb function has been an important topic of study in human evolution, with fossil forelimbs used to interpret the behavior of extinct species and the degree to which they relied on terrestrial bipedalism as a locomotion strategy. This thesis uses biomechanical models and experiments of human walking and running in three studies to investigate how forelimb variation observed in hominin fossils affect the mechanics and costs of bipedal locomotion in order to refine interpretations of the evolution of bipedalism in the hominin lineage.

The first study addressed the question, Why do humans walk with straight arms but run with bent arms? In order to answer the question an experiment was conducted with a modern human sample walking and running with both straight and bent forelimbs. The results of the study indicated that a mechanical tradeoff exists when bending the forelimb at the elbow; bent forelimbs reduce shoulder muscle torque at the cost of increased elbow muscle torque. Net metabolic rate results showed that the mechanical tradeoff favors straight forelimbs during walking, as bent forelimbs increased metabolic rate by 11%. However, the cost of running was equivalent with straight and bent forelimbs, leaving the question of why humans run with flexed elbows unanswered.
The second study addressed the effect of distal forelimb length on the muscle torques at the elbow during walking and running. An experiment was conducted with modern humans walking and running holding hand weights that moved the center of mass of the distal forelimb away from the elbow, experimentally lengthening the segment. Longer distal forelimbs increased the required elbow muscle torque for both gaits, but the effect size was approximately three times greater for running compared to walking. In the hominin fossil record a shift towards relatively shorter distal forelimbs occurred in *Homo erectus*, coincident with the evolution of endurance running. The results of the second study shed light on the evolution of hominin forelimbs, linking forelimb biomechanics during running to selection for shorter distal forelimbs.

The third study addressed functional scaling of forelimb swing dynamics across a range of body sizes and compared functional scaling to geometric scaling of interlimb proportions. Data from an experiment of modern human walking, combined with a theoretical scaling model of shoulder muscle function, indicated that under the constraint of similar shoulder muscle function bigger hominins require relatively shorter forelimbs compared to small variants. Extinct hominin limb proportions are well predicted by the functional scaling model, which outperforms a geometric scaling model that does not incorporate mechanical function. The results of the third study suggest that the shift to relatively short forelimbs in the genus *Homo*, previously interpreted as a signal of a transition from an ancestral mix of arboreal and terrestrial bipedal locomotion to obligate terrestrial bipedalism, is more simply explained as a shift to bigger body size in *Homo*. 
The results of this thesis shed new light on the evolution of human-like walking and running and the origins of the genus Homo. Previous interpretations of hominin locomotion behavior that posit a compromised and costly bipedal gait in hominins before Homo lack biomechanical underpinnings and rely solely on morphological evidence. The results presented here provide the first mechanistic approach to understanding the evolution of hominin forelimbs and lead to the conclusion that human-like walking function evolved in *Australopithecus*, followed by the coincident evolution of larger body size and endurance running in the genus *Homo*. 
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Acknowledgments

Pursuing a Ph.D. is a monumental challenge and journey, with ups and downs and twists and turns throughout years of intense focus on producing new knowledge for the benefit of the scientific and educational communities. I feel truly blessed to have been able to spend the last six years at Harvard chasing my intellectual interests and pursuing my own dream of learning how the world around me works. It’s often said that it takes a village to raise a child, and it truly takes a village to raise a Ph.D. thesis. Below are thanks to some of the many people who helped raise me throughout my time at Harvard.

First, the entire HEB community provided a home for me, and will always truly feel like my academic home. To all the graduate students, postdocs, undergraduates, professors, administrators, and others who make the HEB community such fertile intellectual ground: you are the village that raised me and I owe my career to your nurturing.

I thank the HEB administrators, past and present, in particular: Meg Lynch, Meg Jarvi, Lenia Constantinou, Monica Oyama, Mallory McCoy, and Betty Hughes. You are all the hidden co-authors of my dissertation, and of all the work produced in HEB. Your endless and enthusiastic help in navigating the bureaucracy of Harvard, the grant process, and all the steps that needed to be taken in the past six years smoothed my pathway to my degree so I could walk it while keeping my eye on the prize. I appreciate all you did for me, and I appreciate most your patience with me and your dedication to solving every problem big and small.

To the Skeletal Biology and Biomechanics Lab members: you served as my academic family, and like any loving family you both guided me and challenged me to hone my thinking
and my work, making it the best dissertation it could be. I will always hold the time I had with Carolyn Eng, Brian Addison, Eric Castillo, Eamon Callison, Tory Tobolski, Tim Kistner, Ben Sibson, Anna Warrener, Ian Wallace, Nick Holowka, Katie Zink, and Neil Roach dear in my heart.

I owe limitless thanks to my committee members David Pilbeam, Andrew Biewener, and Madhu Venkadesan for shaping my thesis and providing the constructive feedback and advice that shaped it over several years. Your guidance was critical in honing my mind from that of someone interested in science to that of a scientist, able to form questions and hypotheses with methods to test them.

To my advisor, Dan Lieberman: I can’t use this space to fully explain how much you have meant to my career and my life. The first time we met you welcomed me into your office to discuss my intellectual interests, a meeting I thought would be brief. We ended up talking for over an hour, enthusiastically probing our common interests, and you made me feel in that moment like I belonged in the academic world. Although the Kenya trip that formed from that initial discussion did not make it into this thesis, I am forever grateful that we were able to do an extraordinary project based on that first meeting. You told me my first semester that you would help make an evolutionary biologist out of me, and by golly you did! Your patience, your nurturing, your advice, your ability to take my jumbled ideas and see the way to a formulated plan, are all qualities I will forever appreciate, and you have formed the model for me to be the best professor and advisor I can be in the future.

None of this would have been possible without the lifetime of encouragement from my family. Mom, Dad, Patrick, and Elena: you saw my innate curiosity from the beginning and fostered it at every step of my life. You supported me when I couldn’t stand on my own, both
literally and figuratively. Most importantly you gave me the best examples to be a great thinker, scientist, and person as I grew throughout this process.

Finally, to my loving fiancé, life co-author, and peer review Nesa Wasarhaley: I could write a dissertation on what you mean to me, and will have a lifetime to tell you. Simply, I love you and I appreciate you.
Introduction

Bipedalism is a defining trait in hominins, with evidence of facultative bipedalism in the Miocene (Zollikofer et al., 2005) and human-like walking in the Pliocene (Raichlen et al., 2010). The evolution of bipedalism from an arboreal ancestor with chimpanzees redefined the role of the forelimb in locomotion. Movement in trees as well as terrestrial quadrupedalism involves all four limbs contacting the external environment in order to move the center of mass of the body, while in bipeds the forelimbs produce no contact forces at all. Loss of external contact in the forelimbs is often thought of as "freeing" the limbs from locomotion, and facilitating selection for other tasks, such as carrying infants (Wang and Crompton, 2004), digging, food processing (Zink et al., 2014), tool making (Marzke, 1997), and throwing (Roach et al., 2012). The forelimbs did not lose all function during gait, however, as they have been shown to play an important role in walking and running energetics in humans. Despite growing literature on forelimb locomotion mechanics in modern humans, the connection between bipedal forelimb dynamics and the evolution of hominin forelimbs has not been quantitatively explored until this thesis.

The forelimbs play the important role of counterbalancing angular momentum of the hindlimbs during walking and running in humans (Elftman, 1939; Herr and Popovic, 2008; Hinrichs, 1987). They swing back and forth once per stride and reciprocal to the hindlimbs, conserving angular momentum in the body and limiting the free vertical moment about the center of mass of the body (Collins et al., 2009; Li et al., 2001). This balancing role serves as an energy saving mechanism in walking and running, as perturbation of normal forelimb swing can increase metabolic rate by ~10% (e.g. Arellano and Kram, 2014; Umberger, 2008). Though
forelimb swing saves net energy, it is likely to have a cost as well; hindlimb swing may account for up to one-third the total cost of walking (Doke et al., 2007), and muscles are active in the forelimb during both walking and running (Cappellini, 2006).

Viewed through an evolutionary lens, forelimb anatomy that benefits walking and running by increasing energy savings or reducing cost should be selected for, unless counteracted by a tradeoff with another behavior. The fossil record indicates mosaic evolution of the forelimb in *Australopithecus*, which has been interpreted as evidence of retained climbing behavior in these species (Churchill et al., 2013; Jungers, 2009) and a tradeoff between climbing and walking (e.g. (Jungers, 2009)). The shift to fully modern forelimb anatomy in *Homo* also coincided with the evolution of endurance running (Bramble and Lieberman, 2004), and alternatively may reflect a tradeoff between climbing and running, or non-locomotion behaviors like tool-making and throwing. In order to assess these tradeoff hypotheses about forelimb evolution it is necessary to understand how anatomy affects the costs and benefits of each behavior.

The goal of my thesis was to test hypotheses linking forelimb anatomy to bipedal function, and to interpret evolution of the hominin forelimb in the context of bipedalism. The first three chapters focused directly on the link between anatomy, bipedal forelimb mechanics, and hominin forelimb evolution. In these chapters I addressed two anatomical characters: forelimb length and distal forelimb length.

Chapter 1 asked the question, why do humans walk with straight forelimbs and run with flexed forelimbs? Flexing the elbow into a right angle brings the center of mass of the forelimb closer to the shoulder, effectively shortening forelimb length and reducing the rotational inertia
of the limb. I hypothesized that this behavioral mechanism therefore provides a benefit to walking and running by reducing the cost of swinging the forelimb, but the benefit during walking does not fit with stereotypical behavior in human walking. Therefore, I also hypothesized that a tradeoff exists between the cost at the shoulder and the cost at the elbow, with flexed forelimbs requiring more effort from the elbow muscles, and predicted that metabolic cost would favor the stereotypical behavior in each gait. I tested my hypotheses and prediction using an experiment with people walking and running with both forelimb configurations. The results from the experiment confirm that a tradeoff exists between muscle torque at the shoulder and elbow, with flexed elbows causing reduced shoulder torque and increased elbow torque in both walking and running. Walking with flexed elbows was approximately 11% more costly than with a straight forelimb, as predicted. However, the cost of running was equivalent between both configurations, leaving the reason for flexed elbows during running unknown.

Chapter 2 investigated how variation in distal forelimb length affects walking and running mechanics. Species in the genus Homo including modern humans have relatively short distal forelimbs, a derived feature compared to Australopithecus. The shift to smaller distal forelimbs is first evident in Homo erectus (Richmond et al., 2002), and coincides with a shift towards large day ranges and endurance running (Bramble and Lieberman, 2004). I hypothesized that shortening of distal forelimb would benefit both walking and running by reducing muscle torque at the elbow. To test the hypothesis I conducted an experiment with people walking and running while holding weights in their hands. The addition of mass to the hands lengthened the distance between the center of mass of the distal forelimb and the
elbow, while simultaneously increasing the length of between the center of mass of the entire forelimb and the shoulder. Artificially increasing distal and overall forelimb lengths increased muscle torque at both the shoulder and elbow joints, likely increasing the cost of forelimb swing for both walking and running. However, the effect of relative distal forelimb length on elbow torque was three times greater during running than during walking. In context of the greater effect magnitude in running, the shift to shorter distal forelimbs can be explained by selection for running.

Chapter 3 linked the functions of the forelimbs and hindlimbs during walking in order to test the hypothesis that hominin forelimb lengths can be predicted by modern human walking mechanics. Australopiths had relatively long forelimbs compared to Homo erectus and its descendants (Young et al., 2010), but also had shorter hindlimbs. The same pattern appears in bipedal theropod dinosaurs, which suggests bipedal mechanics may explain the relationship. In order to test the hypothesis I combined a model of hindlimb function, the Froude equation, with a model of forelimb function, the spring-pendulum model, into a new model encompassing both limbs. In order to compare hominins of different sizes I used the framework of dynamic similarity, which standardizes gait across geometric lengths (Alexander and Jayes, 1983). I used an experiment to collect walking data and use the model to predict hominin forelimb lengths across the hindlimb length spectrum. The model prediction could explain the forelimb lengths of all the hominins but the oldest fossil specimen (*Ardipithecus*), and similarly explains theropod dinosaur limb lengths. In light of the results, I hypothesized that bipedalism links selection on limb lengths in bipeds, leading to a predictable relationship between the
limbs that explains why members of the genus *Homo* like modern humans have relatively short forelimbs compared to australopiths.
References


Chapter 1 – Straight arm walking, bent arm running: gait specific elbow angles


Abstract

Stereotypically, walking and running gaits in humans exhibit different arm swing behavior: during walking the arm is kept mostly straight, while during running the arm is bent at the elbow. The mechanism for this behavioral difference has not been explored before. We hypothesized that a mechanical tradeoff exists between the shoulder joint and the elbow joint. Bending the elbow reduces the radius of gyration of the arm and reduces shoulder muscle torque, but at the price of increasing elbow torque. We predicted that the mechanical tradeoff would result in energetics that favored straight arms during walking and bent arms during running. The hypothesis was tested experimentally by having eight subjects walk and run with both straight arms and bent arms while recording arm swing mechanics, and oxygen consumption in a subset of the sample. The mechanical tradeoff hypothesis was confirmed, with bent arms reducing normalized shoulder muscle torque in both gaits (walking: -33%, running: -32%), and increasing normalized elbow muscle torque in both gaits (walking: +110%, running: +30%). As predicted, walking energetics favored straight arms, as bent arms increased oxygen consumption by 11%. However, oxygen consumption was equivalent for both straight and bent arm running conditions, which may be due to changes in metabolic substrate utilization. We conclude that straight arms are stereotyped in walking due to optimal energetics, while the mechanism leading to bent arms during running remains unknown.
Introduction

Although humans swing their arms during both walking and running, elbow angle typically differs between the gaits. Walkers use a "straight arm" with the elbow close to full extension. Runners use a "bent arm" with the elbow flexed and the forearm close to perpendicular with the upper arm. Surprisingly, the reason for this difference is poorly studied. Intuitively, bending the arm when running shortens its length thus reducing the rotational inertia, making it easier and less costly to swing, especially during running when swing frequency is rapid and muscle torques produced at the shoulder are large. However, reducing the effective length of the arm should benefit both walking and running, so a gait-specific mechanism for the difference must exist beyond simply reducing rotational inertia of the entire arm.

Why humans swing their arms during locomotion has been well established: the reciprocal motions of contralateral arm-leg pairs balance angular momentum about the vertical axis internally by transferring momentum between the limbs via the trunk (Bruijn et al., 2008; Collins et al., 2009; Elftman, 1939; Herr and Popovic, 2008). Internal momentum balance reduces the need for an external ground reaction torque at the foot, which is likely to be metabolically costly (Collins et al., 2009; Li et al., 2001; Umberger, 2008a). How humans swing their arms is less well established despite much research. Arm swing can be described as a pendulum operating under a combination of passive and active dynamics (Canton and MacLellan, 2018; Collins et al., 2009; Elftman, 1939; Goudriaan et al., 2014; Kubo et al., 2004; Kuhtz-Buschbeck and Jing, 2012; Meyns et al., 2013). Gravitational torque is a major component of arm swing, as are external driving accelerations that transfer energy from the
legs to the arms via the trunk (Collins et al., 2009; Kubo et al., 2004; Pontzer et al., 2009). At the same time, active muscle recruitment develops torques in the trunk, shoulder, and elbow joints (Ballesteros and Buchthal, 1965; Canton and MacLellan, 2018; Collins et al., 2009; Elftman, 1939; Kuhtz-Buschbeck and Jing, 2012). Neuromuscular control of arm swing is rooted in the central patterns of human gait (Barthelemy and Nielsen, 2010; Cappellini, 2006; Dietz et al., 2001), and may be conserved from quadrupedal ancestry (Dietz, 2002).

Arm swing occurs mainly in the parasagittal plane, yet is linked to angular momentum about the vertical axis. The linkage is partly accomplished by the horizontal joint reaction force at the shoulder ($\mathbf{JRF}_H$) that arises from swing. $\mathbf{JRF}_H$ causes a transverse plane reaction torque ($\tau_{trv}$) on the thorax (Figure 1.1A), which is further linked to the lower body by trunk torsion to transfer momentum between the upper and lower limbs. In the arm, muscle torques occur at the shoulder ($\tau_{sho}$) and the elbow ($\tau_{elb}$), generally opposing angular excursion and acting in a resistive manner (Collins et al., 2009) (Fig. 1.1A). $\tau_{sho}$ is most simply explained as resembling a rotational spring and acting on a functionally rigid single pendulum arm. Bending the elbow moves the center of mass (CoM) of the pendulum closer to the shoulder pivot, reducing the radius of gyration ($R_G$) and the required $\tau_{sho}$ (Figure 1.1B).

In order to maintain functional approximation of a single pendulum arm, $\tau_{elb}$ must resist external forces that would cause an external torque at the elbow and rotation of the forearm relative to the upper arm. Gravity is one such external force. Pseudoforces from acceleration of the thorax also place external torques on the forearm in the reference frame of the upper arm. Vertical acceleration measured at the shoulder has a much higher magnitude compared to horizontal acceleration in walking (Kubo et al., 2004). Similarly, measurements of linear
Figure 1.1 Illustration of the mechanical tradeoff hypothesis. A: three relevant torques (curved arrows) occur during arm swing: muscle torque at the elbow ($\tau_{elb}$), muscle torque at the shoulder ($\tau_{sho}$), and transverse reaction torque on the thorax ($\tau_{trv}$) arising from the horizontal joint reaction force at the shoulder ($JRF_{sh}$, straight arrow). B: when the arm is bent at the elbow the center-of-mass of the arm moves closer to the shoulder joint, reducing rotational inertia of the arm and the burden on the shoulder muscles. C: at the same time, the moment arm (dashed line) for vertical external forces acting on the forearm increases with the bent arm, increasing the burden on the elbow muscles.
displacements at C7 vertebral level indicate larger vertical than horizontal accelerations in both walking and running (Thorstensson et al., 1984). Other forces causing external elbow torques arise from centripetal and tangential accelerations of the elbow joint center in the arm reference frame. The net effect of all these forces is likely a large vertical external force component contributing to the external elbow torque, and a smaller horizontal component. Bending the elbow to reduce arm $R_g$ brings the forearm closer to horizontal, thus increasing the moment arm of the net vertical external force (Figure 1.1C). Conversely, maintaining a straight arm places the forearm more parallel with the vertical forces, limiting the external torque they produce and consequently the resistive $\tau_{elb}$.

We propose a mechanical tradeoff hypothesis that posits a tradeoff between muscle torques at the shoulder and the elbow linked to the average elbow angle. Flexing the elbow, thus shortening the arm’s moment of inertia, reduces the shoulder muscle torque but at the cost of increasing the elbow muscle torque. We predict that the energetic consequences of the mechanical tradeoff favor straight arm walking and bent arm running, and that elbow angle is determined by energetic cost for each gait. Studies of both walking and running show that perturbation of normal arm swing, typically by holding or binding the arms to the torso, increases the net energy cost of locomotion by up to 10% in walking (Collins et al., 2009; Ortega et al., 2008; Umberger, 2008a) and running (Arellano and Kram, 2014; Egbuonu et al., 1990; Tseh et al., 2008), indicating that normal arm swing is an important cost-saving mechanism. We also predict similar non-trivial energy costs to altering normal elbow angle. We tested our hypothesis and predictions by conducting an experiment with human subjects who walked and ran with both flexed and extended elbows.
**Methods and Materials**

Eight healthy subjects (four males and four females, age: 26.6 years, s.d. 2.5, mass: 76.6 kg, s.d. 15.9) participated in the experiment. Prior approval was granted by the Harvard University Institutional Review Board, and all subjects gave informed consent. Subjects walked and ran on a split-belt treadmill instrumented with force plates (Bertec Corp., Columbus, Ohio). Four randomized experimental conditions were conducted in random order: straight arm walking (SW), bent arm walking (BW), straight arm running (SR), and bent arm running (BR). For SW and BR the subjects were asked to walk and run normally. For BW subjects were instructed to hold their forearm as they would during running; similarly, the instruction for SR was to hold the forearm as they would during walking. All walking trials were done at a single dimensionless speed (Froude = 0.2, range: 1.30 m/s to 1.44 m/s), and running trials were also done at a single dimensionless speed (Froude = 1, range: 2.90 m/s to 3.22 m/s). Each condition lasted three minutes, with data collection occurring during the last minute. Six subjects returned within two weeks for energetic data collection (see below). All analyses used the Igor Pro software platform (Wavemetrics, Lake Oswega, Oregon).

*Kinematic and Kinetic Time Series*

Motions of the right forearm, right upper arm, and the thorax were captured with eight infrared cameras recording at 200 Hz (Qualysis Motion Capture Systems, Gothenburg, Sweden). Reflective markers were placed on the left and right acromia, right humeral epicondyles, and right radial and ulnar styloid processes. The right shoulder joint was estimated to be 3.0
(females) or 3.5 cm (males) below the right acromion marker (De Leva, 1996). The elbow joint center was calculated as the midpoint between the humeral epicondyles, and the wrist joint center was calculated as the midpoint between the styloid processes. The radius of the thorax was estimated as half the distance between the left and right acromia. Raw time series were filtered using a 10 Hz low pass filter.

Analyses were done on the right arm segments in a parasagittal plane. Shoulder angle ($\theta_{sho}$, rad) was defined as the angle formed by the upper arm and the vertical. Elbow angle ($\theta_{elb}$, rad) was defined as the angle formed by the forearm and upper arm, with a straight arm being the neutral position. Angles followed the Right Hand Rule, with positive angles representing flexion. Segmental inertias for the forearm and upper arm were estimated using subject metrics and anthropometric tables (De Leva, 1996). Standard inverse dynamics equations were used to calculate joint reaction forces, $\tau_{sho}$ (Nm), and $\tau_{elb}$ (Nm) (Winter, 2009). $JRF_H$ (N) was multiplied by the radius of the thorax in meters to yield $\tau_{trv}$ (Nm). Right heel strikes were used to define strides, and were determined from the vertical force traces under the right foot. Ten consecutive strides were averaged for each subject and condition. Inter-subject stride averages and standard errors were then calculated.

Kinetic variables were extracted from the individual stride averages. Magnitudes of each torque ($\Delta \tau_{trv}$, $\Delta \tau_{sho}$, and $\Delta \tau_{elb}$) were calculated as the difference between the maximum and minimum values across the stride. $\Delta \tau_{sho}$ and $\Delta \tau_{elb}$ were normalized to dimensionless muscle torques $\Delta T_{sho}$ and $\Delta T_{elb}$ by dividing by $\Delta \tau_{trv}$. Inter-subject means and standard errors were calculated for each variable.
Energetics Data Collection

Following the initial experiment, six of the original subjects returned within two weeks and repeated the experiment while we collected metabolic data. Energetics were measured via oxygen consumption using an open-flow respirometry system (Sable Systems, North Las Vegas, Nevada, USA) and standard equations (Withers, 1977).

Resting oxygen consumption was recorded first, with the subject standing quietly on the treadmill. The four experimental conditions followed in a randomized order. Each condition, including rest, lasted for five minutes. Average oxygen consumption across the last two minutes was extracted to represent steady-state energetics. Oxygen consumption rates were normalized using body mass, and resting metabolism was subtracted from the walking and running conditions to calculate net oxygen consumption, $\dot{E}_{net}$ (W/kg).

Statistics

Comparisons between experimental condition means were done for walking and running separately: SW v. BW and SR v. BR. Repeated measures ANOVA (threshold p=0.05) was used to assess for statistical differences between mean values for $\Delta T_{trv}$, $\Delta T_{sho}$, $\Delta T_{elb}$, and $\dot{E}_{net}$.

Results

Transverse Reaction Torque

In all four conditions, $\tau_{trv}$ showed a consistent pattern of peak clockwise torque near ipsilateral heel strike and peak counter-clockwise torque near contralateral heel strike (Figure 1.2A and 1.2B), with both occurring mainly at stride frequency. Comparison between the
Figure 1.2 Comparison of transverse reaction torques between experimental conditions. A: inter-subject averages across the stride for walking, B: running. Black lines represent straight arm conditions, grey lines bent arm conditions. Shaded bands are ± one standard error. C: magnitudes of transverse reaction torques across the stride. Dark grey: straight arm conditions, light grey: bent arm conditions. Error bars are ± one standard error.
magnitudes of the torques (Figure 1.2C) yielded no significant difference within the walking conditions (p=0.29) or the running conditions (p=0.19).

Shoulder

In both walking and running, $\theta_{sho}$ followed a stride-frequency pattern with peak flexion occurring near contralateral heel strike (Figure 1.3A and 1.3B). The magnitudes of angular excursion tended to be similar within each gait. However, BW tended to shift $\theta_{sho}$ towards extension compared to SW, while BR tended to shift towards flexion compared to SR. $\tau_{sho}$ also followed a stride-frequency pattern (Figure 1.3C and 1.3D), with peak extension torques coinciding with peak shoulder flexion. ANOVA tests showed 33% reduced $\Delta T_{sho}$ in BW compared to SW (p=0.0039), and 32% reduced BR compared to SR (p<0.0001) (Figure 1.3E).

Elbow

Consistent with the instructions given to the subjects, $\theta_{elb}$ was substantially more flexed in BW and BR compared to SW and SR (Figure 1.4A and 1.4B), and the forearm was close to perpendicular ($\theta_{elb} = 1.57$ rad) with the upper arm. Mean $\theta_{elb}$ in SW and BW were $0.62 \pm 0.02$ radians and $1.54 \pm 0.05$ radians respectively (p<0.0001). Mean angles were similar in running, with $0.61 \pm 0.05$ radians and $1.61 \pm 0.10$ radians in SR and BR respectively (p<0.0001). Both gaits showed angular excursions occurring at stride frequency. However, unlike in the shoulder, the pattern of $\theta_{elb}$ across the stride differed between straight and bent arm conditions. In SW and SR the elbow flexed near contralateral heel strike, while in BW and BR the elbow extended when the opposite foot hit the ground. $\tau_{elb}$ followed stride frequency patterns for SW and SR,
Figure 1.3 Comparison of shoulder angles and muscle torques between experimental conditions. A: shoulder angle across the stride for walking conditions, B: running conditions. C: shoulder muscle torque across the stride for walking conditions, D: running conditions. Black lines represent straight arm conditions, grey lines bent arm conditions. Shaded bands are ± one standard error. E: normalized magnitudes of shoulder muscle torques. Dark grey: straight arm conditions, light grey: bent arm conditions. Error bars are ± one standard error. Asterisks indicate statistically significant differences between straight arm and bent arm conditions within each gait.
Figure 1.4 Comparison of elbow angles and muscle torques between experimental conditions. A: elbow angle across the stride for walking conditions, B: running conditions. C: elbow muscle torque across the stride for walking conditions, D: running conditions. Black lines represent straight arm conditions, grey lines bent arm conditions. Shaded bands are ± one standard error. E: normalized magnitudes of elbow muscle torques. Dark grey: straight arm conditions, light grey: bent arm conditions. Error bars are ± one standard error. Asterisks indicate statistically significant differences between straight arm and bent arm conditions within each gait.
but step frequency patterns for BW and BR (Figure 1.4C and 1.4D). In addition, mean muscle torques were substantially shifted towards flexion in the bent arm conditions (on average, 1.21 Nm in walking and 1.60 Nm in running), presumably due to increased gravitational torque. Comparison of magnitudes yielded significant increases in $\Delta T_{elb}$ for the bent arm conditions compared to the straight arm conditions in both walking (110% increase, $p=0.0037$) and running (30% increase, $p=0.0096$) (Figure 1.4E).

**Energetics**

Figure 1.5 shows the results from the energetics data collection on the six-subject subsample. BW incurred a 11±3% higher $\dot{E}_{net}$ than SW ($p=0.0175$), increasing by 0.30 W/kg compared to the normal SW condition. In contrast, $\dot{E}_{net}$ was the same for the SR and BR conditions ($p=0.67$).

**Discussion**

The results from our experiment confirm the hypothesis that there is a tradeoff between $\tau_{sho}$ and $\tau_{elb}$ when bending the arm at the elbow during locomotion. Bending the arm reduced the relative magnitude of the shoulder muscle moment in both walking and running (Fig. 1.3E), while simultaneously increasing the relative magnitude of the elbow muscle moment (Fig. 1.4E). Our hypothesis focuses on the vertical external forces that cause an external torque on the forearm resisted by $\tau_{elb}$. The stride time series of $\tau_{elb}$ (Fig. 1.4C and 1.4D) shows the effect of bending the elbow and bringing the forearm more perpendicular to the net vertical external force. In BW and BR, $\tau_{elb}$ showed a step frequency pattern similar to vertical
Figure 1.5 Net metabolic energetics during walking and running. Dark grey bars represent straight arm conditions, while light grey bars represent bent arm conditions. Error bars are ± one standard error. Asterisk indicates a statistically significant difference between straight and bent arm conditions within a gait.
accelerations of the trunk (Kubo et al., 2004; Thorstensson et al., 1984). Conversely, $\tau_{elb}$ oscillated at stride frequency in SW and SR, likely due to swinging of the upper arm (Fig. 1.3A and 1.3B) dominating the external torque acting on the forearm.

We predicted that the gait-specific stereotypical behaviors of straight arm walking and bent arm running are driven by the energetic consequences of the mechanical tradeoff, with walking favoring straight arms and running favoring bent arms. The first part of our prediction was supported by our data (Fig. 1.5), as walking with a bent arm increased $E_{net}$ by 11%, similar to the magnitude of cost increase caused by restricting arm swing (Bruijn et al., 2008; Collins et al., 2009; Umberger, 2008b). However, while we predicted $\dot{E}_{net}$ would be reduced in bent arm running, our results show the same metabolic cost between the two elbow angle conditions (Fig. 1.5).

We surmise three possible reasons the running prediction was not supported. First, we tested only a single dimensionless speed, and it is possible that running becomes less costly with bent arms than straight arms at higher speeds than we tested. Although elbow angle did not affect the net cost of running, higher torques were generated by the shoulder muscles with straight arms compared to bent, requiring more activated muscle volume. Larger and costlier motor units tend to be activated as more volume is recruited in muscle contractions (Duchateau and Enoka, 2011), so it is possible that fiber recruitment order affects the tradeoff at faster speeds. Second, there may be an independent benefit to bending the arms when running, such as creating a linkage between the biceps and cleidocranialtrapezius muscles for the purpose of head stabilization (Lieberman, 2011). Testing for speed effects within each gait may shed more light on our running energetic results. Third, our analysis was limited to
parasagittal arm swing. Bending the elbow affects frontal and transverse plane mechanics; however, any change in mechanics in those two planes already factor into the net energetics, so the change would have to provide a non-energetic benefit to be the reason for the typical running elbow angle.

There is a clear energetic benefit to keeping the arms straight when walking, making straight arms the "optimal" configuration. Lack of an energetic benefit for either elbow angle in running means that there is no "optimal" configuration per se. Even though bent arms are stereotyped in running, exactly how the forearm is carried seems to matter little when it comes to energetics. To that end, there was much greater variation within our sample in average $\theta_{elb}$ for the normal running condition (s.d. of 0.274 rad) than the normal walking condition (s.d. 0.070 rad), matching our anecdotal observation that runners use quite varied forearm positions.

In light of our results, we hypothesize that bent arms are stereotyped during running in order to increase endurance running capacity. The evolution of endurance running in the genus Homo was a major transition in the course of human evolution (Bramble and Lieberman, 2004). The capacity to run very long distances at speeds that force galloping in prey mammals was a critical innovation in hunter-gatherer ecology. In our experiment, elbow angle did not affect the instantaneous metabolic power of running, suggesting the metabolic savings at the shoulder via bending the arms were balanced by the metabolic costs at the elbows. However, the two conditions had very different relative burdens between the shoulder and elbow muscles. Straight arm running requires large shoulder muscle torques and relatively small elbow muscle torques, while during bent arm running the torque burden is more equitable between the
joints. Equitable sharing of the muscular burden between the two joints may reduce the rate of metabolite buildup and fatigue in the shoulder muscles, and may increase endurance capabilities. This hypothesis should be tested in a further experiment.

Finally, our results have implications for the evolution of arm proportions in hominins. Arm length relative to leg length was greater in *Australopithecus* and in *Homo habilis* compared to modern humans (Young et al., 2010), as was forearm length relative to upper arm length (Churchill et al., 2013; Richmond et al., 2002). Modern arm proportions emerged in *Homo erectus*, and coincided with the evolution of endurance running as an important hominin behavior (Bramble and Lieberman, 2004). Reductions in forearm length and total arm length should reduce $\tau_{elb}$ and $\tau_{sho}$, respectively, and therefore may be signals of selection for lesser arm swing costs during endurance running. Selection for running may have been an important factor shaping the evolution of hominin arms.

**Acknowledgments**

We thank Andrew Biewener, Nicholas Holowka, Ian Wallace, Eamon Callison, and Victoria Tobolsky for helpful comments at various stages of the project. We also thank the anonymous reviewers for their comments and improvements on the manuscript.

**Funding**

Funding was provided by the Robert A. Chapman Memorial Scholarship for Vertebrate Locomotion (AKY, Harvard University), and the American School of Prehistoric Research (DEL, Harvard University).
References


Chapter 2 - Shorter distal forelimbs reduce elbow and shoulder torques during bipedal walking and running.

Abstract

Early hominins such as australopiths had distal forelimb lengths similar to extant apes, as measured by the brachial index. A shift to smaller distal forelimbs occurred in Homo erectus, contemporaneous with evolution of the hunter-gatherer way of life. We hypothesized that shorter distal forelimbs benefit walking and running, and predicted that the benefit would be greater in running compared to walking. We tested the hypothesis in modern humans walking and running while carrying hand weights. The hand weights increased the effective length of the distal forelimb, simulating a larger brachial index. We found longer distal forelimbs increased elbow muscle torque by 98% while walking and 70% in running, confirming our hypothesis that shorter distal forelimbs benefit walking and running. Shoulder muscle torque similarly increased in both gaits with the addition of hand weights due to elongation of the effective forelimb length. Normalized elbow torque, which accounted for the effect on shoulder torque caused by the experimental manipulation, increased by 16% while walking but 52% while running, indicating that shorter distal forelimbs provide a greater benefit for running by approximately three-fold. Large day ranges and the evolution of endurance running in Homo likely contributed to the shift towards relatively smaller distal forelimbs, which were retained in more recent species including modern humans.

Introduction
There has been strong selection on limb structure and function in all vertebrates, but limb variation is especially interesting in hominins given the evolution of terrestrial bipedalism from a more arboreal common ancestor with chimpanzees (Gebo, 1996; Richmond et al., 2002b; Thorpe et al., 2007; Lovejoy et al., 2009; Pilbeam and Lieberman 2017). A longstanding, common method for categorizing primate limb anatomy is the use of long bone ratios (Schultz 1937), which facilitate body plan comparisons among individuals and species by using size-normalized indices (Richmond et al., 2002a; Reno et al., 2005; Young et al., 2010). One such index is the brachial index (BI), defined as the ratio of distal forelimb length (radius length) over proximal forelimb length (humerus length), indexed to 100. Fossil evidence suggests that for the first several million years of hominin evolution BI was variable but within the range of means for extant great apes, between the lower limit of Gorilla (BI=80) and the upper limit of Pongo (BI=101), and mostly clustered between 82-90 (Table 2.1, Figure 2.1). Homo habilis (OH 62) may have had a BI of ~86, but the emergence of Homo erectus in Africa around 1.9 m.y.a. was accompanied by a shift to a BI of ~80 (represented by KNM-WT 15000), at the edge of the range of extant great apes (Fig. 1). BIs in the range of approximately 73 to 78 have since persisted in other more recent species of the genus Homo including Homo sapiens (Fig. 1). This shift in BI coincided with a suite of additional anatomical changes first evident in H. erectus linked to the evolution of a hunter-gatherer way of life that included large day ranges, endurance running, and throwing (Hawkes et al., 1997; Bramble and Lieberman, 2004; Robson and Wood, 2008; Roach et al., 2014; Hawkes et al., 2018) Because apes have larger BIs than humans and are generally adapted for arboreal locomotion, there is ongoing debate whether
### Table 2.1 Comparative Brachial Indices in hominins and hominoids.

<table>
<thead>
<tr>
<th>Classification</th>
<th>Fossil</th>
<th>Date (mya)</th>
<th>Humerus (m)</th>
<th>Radius (m)</th>
<th>Brachial Index</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ar. ramidus</em></td>
<td>ARA-VP-6/500</td>
<td>4.4</td>
<td>0.278</td>
<td>0.250</td>
<td>90</td>
<td>a</td>
</tr>
<tr>
<td>Au. <em>spp</em></td>
<td>StW 573</td>
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<td>0.240</td>
<td>83</td>
<td>b</td>
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<td><em>Au. aferensis</em></td>
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<td>0.237</td>
<td>0.210</td>
<td>89</td>
<td>c, d</td>
</tr>
<tr>
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<td>BOU-VP-12</td>
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<td>0.236</td>
<td>0.231</td>
<td>98</td>
<td>e</td>
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<tr>
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<td>2.0</td>
<td>0.269</td>
<td>0.220</td>
<td>82</td>
<td>f, g</td>
</tr>
<tr>
<td><em>H. habilis</em></td>
<td>OH 62</td>
<td>1.8</td>
<td>0.264</td>
<td>0.228</td>
<td>86</td>
<td>c</td>
</tr>
<tr>
<td><em>H. erectus</em></td>
<td>KNM-WT-15000</td>
<td>1.5</td>
<td>0.319</td>
<td>0.255</td>
<td>80</td>
<td>c</td>
</tr>
<tr>
<td><em>H. floresiensis</em></td>
<td>LB1</td>
<td>0.09</td>
<td>0.243</td>
<td>0.190</td>
<td>78</td>
<td>h, i</td>
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<tr>
<td><em>H. neanderthalensis</em></td>
<td>La Ferrassie 1</td>
<td>0.04</td>
<td>0.335</td>
<td>0.243</td>
<td>73</td>
<td>j</td>
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<tr>
<td><em>Pongo</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>102</td>
<td>k</td>
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<tr>
<td><em>Gorilla</em></td>
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<td><em>Pan</em></td>
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<td>93</td>
<td>k</td>
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<tr>
<td><em>H. sapiens</em></td>
<td></td>
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<td></td>
<td></td>
<td>76</td>
<td>k</td>
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</tbody>
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a. Lovejoy et al. (2009)  
b. Heaton et al. (bioRxiv)  
c. Richmond et al. 2002  
d. Haile Selassie et al. (2010)  
e. Aswaf et al. (1999)  
f. DeSilva et al. (2010)  
g. Churchill et al. (2013)  
h. Jungers et al. (2009)  
j. Trinkaus (1981); Guerin et al. (2015) [date]  
k. Schultz (1937)
Figure 2.1 The shift in hominin Brachial Index across time. Closed symbols are extant hominoids, open symbols fossil hominins. Estimates used in the figure are listed in Table 2.1. Until the early Pleistocene, hominin brachial index values fell within the range of apes (Pre-Shift, green shaded region and symbols). A shift towards smaller brachial indices is first evident ~1.5 mya and retained in more recent species (Post-Shift, red shaded region and symbols).
fossil BIs can provide diagnostic information about the behavior of extinct hominins (e.g. see (Churchill et al., 2013))

There are several potential hypotheses to explain the shift to lower BIs in Homo. One possible mechanism is developmental integration between the forelimb and hindlimb elements (Young et al., 2010). If so, selection for relatively shorter distal hindlimbs would lead to shorter distal forelimbs, and consequently a lower BI. One problem with this hypothesis is lack of variation and evidence for directional change in the analogous hindlimb skeletal index (Crural Index: distal hindlimb over proximal hindlimb) (Richmond et al., 2002a; Haile-Selassie et al., 2010). Selection driven by thermoregulation has previously been hypothesized to contribute to distal limb evolution (e.g. (Holliday, 1997)). However, in the hot, arid environments of Africa the thermoregulation hypothesis predicts distal limb elements should get relatively longer, not shorter as observed in the fossil record. Another potential hypothesis is that selection for derived manual mechanical tasks such as tool making, and perhaps overhand throwing (Roach and Lieberman, 2014; Roach et al., 2014), favored higher BIs. However, these and other tasks that require acceleration of the hand would seemingly benefit from longer distal forelimbs rather than shorter ones by transferring more momentum to the grasped object, although quantitative tests of this mechanical hypothesis are lacking. Furthermore, the relationships between distal forelimb length and the control or accuracy of manual tasks have not been modeled to date.

Here we explore a final hypothesis for the directional shift towards smaller BIs: that smaller BI benefits bipedal walking and running mechanics. During walking and running humans swing their forelimbs in order to counterbalance the angular momentum of the
hindlimbs, increasing stability and reducing the energetic cost of locomotion (Elftman, 1939; Hinrichs, 1987; Herr and Popovic, 2008; Umberger, 2008; Collins et al., 2009). The entire forelimb swings about the shoulder joint like a single pendulum under the control of a shoulder muscle torque ($\tau_{\text{sho}}$) produced by the deltoid and other muscles (Yegian et al., prepared). The effective length of the single pendulum forelimb (Figure 2.2A) is the fundamental determinant of how much muscular effort at the shoulder is required to swing the limb (Yegian et al., prepared). However, the forelimb is not a single pendulum because motion can also occur at the elbow joint. In order to allow the forelimb to act like a single pendulum during gait the elbow is kept mostly rigid by muscles (Figure 2.2B), resulting in an elbow muscle torque ($\tau_{\text{elb}}$) (Yegian et al., prepared). Muscle contractions needed to develop torques cost metabolic energy, so both $\tau_{\text{sho}}$ and $\tau_{\text{elb}}$ contribute an unknown, but likely modest, amount to the cost of locomotion.

Because only $\tau_{\text{sho}}$ contributes to counterbalancing momentum, morphology that reduces $\tau_{\text{elb}}$ for a given $\tau_{\text{sho}}$ in theory provides an energetic benefit, and we hypothesize that forelimb variants that produce this outcome might be favored by selection if substantial enough benefits exist. The obvious candidate for such a mechanism is reduced length of the distal forelimb, which reduces inertia. Rotational inertia of a segment is defined in the simplest case as $mL^2$, with $m$ being the mass of the segment and $L$ the length between the joint and the segment center of mass. For a given angular motion of a segment about a joint, muscle torque and the resulting energy cost are positively related to the rotational inertia of the segment. Reducing $L$ and moving the center of mass closer to the joint reduces inertia and consequently reduces the muscle torque and energy cost of the motion. All else being equal, smaller BI values indicate a
Figure 2.2 Schematic of the forelimb joint muscle torques during gait. (a) Shoulder torque (red arrow showing extension) produced by muscle activation controls motion of the pendulum-like forelimb, with an effective length (black line) equal to the distance between the center of mass of the forelimb and the shoulder joint. (b) Elbow torque (blue arrow showing flexion) controls motion of the distal forelimb, which similarly has an effective length (black line) defined by the position of the center of mass of the segment.
relatively shorter distal forelimb, and therefore should reduce the relative magnitude and cost of $\tau_{elb}$ during locomotion.

In addition to the hypothesis that a smaller BI reduces the joint torques generated during walking and running, we also hypothesize that the benefit for running is greater than for walking. While walking, humans tend to keep their elbows mostly straight, but while running the elbows are usually bent to approximately $90^\circ$ thus decreasing the forelimb’s effective length (Yegian et al., Chapter 1). This bent elbow strategy, however, orients the distal forelimb more horizontally and thus perpendicular to the gravitational force. Gravity acts to push the elbow toward extension, and must be resisted by elbow muscles and $\tau_{elb}$. In addition, the magnitude of $\tau_{elb}$ compared to $\tau_{sho}$ is greater in running than in walking (Yegian et al., Chapter 1). Taken together, relatively shorter distal forelimbs likely provides a greater benefit for running than walking.

To test the hypothesis that a shorter distal forelimb (i.e. smaller BI) decreases the external moments generated at the shoulder and elbow in walking and even more so in running we conducted an experiment using a within-subject design, artificially manipulating the distal forelimb inertia of the participants by having them hold hand weights. Hand weights shift the center of mass of the distal forelimb away from the elbow, increasing the effective length of the segment and its inertia. Within-subjects design controlled for inter-subject variation in other gait variables, while the inertial manipulation approach allowed for testing greater variation than possible with a between-subjects comparative approach, increasing the resolution for detecting a trend. Note that the experiment did not directly alter BIs between treatments because BI is strictly defined as a skeletal ratio, but instead the hand weight conditions
produced an approximate heuristic of a larger BI and the resulting effect on $\tau_{elb}$. However, the hand weights also increased the inertia of the entire forelimb, which affects $\tau_{sho}$. We therefore normalized $\tau_{elb}$ by dividing by $\tau_{sho}$, yielding a dimensionless normalized elbow muscle torque ($T_{elb}$) that accounts for the effect of the added mass on the swing dynamics of the whole forelimb and the control of swing by the shoulder muscles. We then compared the magnitude of each torque across the stride for normal walking and running to that with added distal forelimb inertia, and compared the effect size of walking to that of running.

**Methods and Materials**

Eight humans (four males and four females, age: 26.6 years, s.d. 2.5, mass: 76.6 kg, s.d. 15.9) with no musculoskeletal injuries or illnesses were participants in this experiment. The Harvard University Institutional Review Board approved the experiment, and all participants provided informed consent. During the experiment participants walked and ran on a force plate-instrumented treadmill (Bertec Corp., Columbus, Ohio) at speeds ranging between 1.30 m/s to 1.44 m/s for walking, and 2.90 m/s to 3.22 m/s for running. Treadmill speeds were calculated individually by using dimensionless speeds (Froude numbers) of 0.2 for walking and 1.0 for running.

In order to test the effects of brachial inertia on walking and running mechanics, we asked the participants to walk and run normally as well as with three pound (1.36 kg) weights in each hand. Each participant therefore was measured during four experimental conditions in random order: normal walking (W), walking with added mass (W+M), normal running (R), and running with added mass (R+M). Each trial lasted three minutes, and data were collected during
the last minute after acclimatization. Modeling and data analysis were conducted using the Igor Pro software platform (Wavemetrics, Lake Oswega, Oregon).

Data collection consisted of motion capture of the right arm during locomotion. Small infrared reflective markers were taped to the skin over the following bony landmarks: radial styloid process, ulnar styloid process, lateral humeral epicondyle, medial humeral epicondyle, and acromion. Eight infrared cameras tracked the motions of the markers in three-dimensional space at a sampling frequency of 200 Hz (Qualysis Motion Capture Systems, Gothenburg, Sweden). When added mass was used, markers were placed on the ends of the hand weights. The location of the wrist joint was defined as the midpoint between the styloid processes, the elbow joint was defined as the midpoint between the humeral epicondyles, and the shoulder joint was estimated to be 3.0 (females) or 3.5 cm (males) below the acromion marker (De Leva, 1996). The location of the added mass was defined as the midpoint of the hand weight. The data were reduced to only sagittal plane motions, and the raw time series were filtered using a zero-lag 10 Hz low pass binomial smoothing filter. In addition to the kinematic data, vertical force traces were obtained to define start and endpoints of individual strides. Ten consecutive strides were identified and averaged for each subject and condition.

The forelimb was modeled as a two-segment system consisting of the proximal forelimb and the distal forelimb, with the latter including the hand. Shoulder ($\theta_{sho}$) and elbow joint ($\theta_{elb}$) angles were calculated from the joint positions. Inertial properties of the arm segments were estimated using individual subject measurements and standard anthropometric tables (De Leva, 1996). In the added mass conditions the mass of the hand weight was included in the inertia of the distal forelimb. Kinematics and inertia were then combined in a standard inverse
dynamics model (Winter, 2005) in order to obtain the muscle torques at the shoulder ($\tau_{sho}$) and elbow ($\tau_{elb}$) joints. The magnitudes of the muscle torques ($\Delta \tau_{elb}$ and $\Delta \tau_{sho}$, defined as the difference between maximum and minimum torque during the stride) were extracted, and the normalized elbow torque, $T_{elb}$, was calculated as the ratio of $\Delta \tau_{elb}$ over $\Delta \tau_{sho}$. In addition, the effective length of the forelimb was calculated using the positions of the individual segment masses and the shoulder joint. Inter-subject means of $\Delta \tau_{elb}$, $\Delta \tau_{sho}$, and $T_{elb}$ were compared between the added mass conditions (W+M and R+M) and the normal conditions (W and R) using repeated measures ANOVA with significance based on standard $\alpha=0.05$. Linear regression was used to confirm that $\Delta \tau_{sho}$ was directly related to effective forelimb length.

**Results**

Joint kinematics and kinetics across the stride for the walking conditions are presented in Figure 2. In stereotypical forelimb kinematics during walking, $\theta_{elb}$ and $\theta_{sho}$ reach peak flexion near mid-stance, with the forelimb at its most anterior point around contralateral heel strike (50% of stride). $\tau_{elb}$ and $\tau_{sho}$ both show markedly greater peaks during the stride in W+M condition compared to normal walking (W). $\Delta \tau_{elb}$ increased by 98% on average with the added mass (W: 1.72 ± 0.31; W+M: 3.40 ± 0.71; p=0.009; Nm units and standard error for all results unless noted), while $\Delta \tau_{sho}$ increased by 77% on average (W: 4.48 ± 0.63; W+M: 7.94 ± 1.64; p=0.016).

Figure 2.4 presents the same variables for the running conditions. In contrast with walking, $\theta_{elb}$ underwent slight extension near contralateral heel strike (~30-40% of stride), while $\theta_{sho}$ reached peak flexion at the same time. As in walking, peak torques were noticeably greater
Figure 2.3 Elbow and shoulder kinematics and kinetics during walking conditions. Black traces represent normal walking (W), while grey traces represent walking with added mass in the hand (W+M). Shaded bands and error bars represent one standard error of the mean. (a) Elbow angle (b) elbow torque (c) the change in elbow torque across the stride. (d) Shoulder angle (e) shoulder torque (d) the change in shoulder torque across the stride. The results of t-tests comparing mean values are given in (c) and (f). Angles and torques are defined as positive for flexion, negative for extension.
Figure 2.4 Elbow and shoulder kinematics and kinetics during running conditions. Black traces represent normal walking (R), while grey traces represent walking with added mass in the hand (R+M). Shaded bands and error bars represent one standard error of the mean. (a) Elbow angle (b) elbow torque (c) the change in elbow torque across the stride. (d) Shoulder angle (e) shoulder torque (d) the change in shoulder torque across the stride. The results of t-tests comparing mean values are given in (c) and (f). Angles and torques are defined as positive for flexion, negative for extension.
with added mass. When running with added mass, $\Delta T_{\text{elb}}$ significantly increased by 70% compared to normal (R: 10.69 ± 1.72; R+M: 18.18 ± 2.75; p=0.004), a similar proportional increase as walking. In contrast, adding mass to the forearm increased $\Delta T_{\text{sho}}$ by only 10% (R: 16.26 ± 3.28; R+M: 17.91 ± 2.82; p=0.019).

As predicted, linear regressions through individual subject data pooled by gait show strong correlations between $\Delta T_{\text{sho}}$ and effective forelimb length (Figure 2.5). The trend through the walking data had a slope of 2.65 Nm/m (p<0.001; $r^2=0.69$), while the trend through the running data had approximately twice the effect size, with a slope of 5.64 Nm/m (p<0.001; $r^2=0.74$). There were significant increases in relative elbow muscle effort with added inertia for both gaits (Figure 2.6) as measured by dimensionless elbow torque, $T_{\text{elb}}$, which controlled for the relationship between $\Delta T_{\text{sho}}$ and effective forelimb length. When walking, the added inertia increased $T_{\text{elb}}$ by 16% (W: 0.38 ± 0.03; W+M: 0.44 ± 0.03; p=0.021). In contrast, added inertia during running increased $T_{\text{elb}}$ by 52% (R: 0.66 ± 0.05, R+M: 1.00 ± 0.11, p=0.009). Therefore, the same added inertia had ~3x the effect on elbow torque during running compared to walking.

Discussion

The experimental results presented here support the hypothesis that reduced distal forelimb inertia benefits both walking and running by reducing muscle torque and presumably effort required by elbow muscles during gait to counteract torques acting on the elbow. Because distal forelimb inertia is positively related to BI, this provides support for the hypothesis that reduced BI benefits both walking and running by reducing the effort needed to stabilize the elbow. While our experiment illustrated the directional effect and mechanical
Figure 2.5 Relationship between shoulder torque and effective forelimb length. Walking conditions are represented by closed symbols, running conditions by open symbols. Linear regression through the walking data is indicated by the solid line, and regression through the running data by the dashed line.
Figure 2.6 Mean normalized elbow torque during walking and running conditions. Normalized elbow torque was calculated as the ratio of elbow torque over shoulder torque, and accounts for changes in the effective length of the forelimb. Results of t-tests comparing means between conditions for walking and running are given in the figure.
benefit of reduced BI, further research is needed to quantify the magnitude of the effect on the cost of locomotion, or facilitate functional comparisons between hominins with different BIs. However, by comparing the same inertial manipulation between walking and running in the same subjects, we were able to observe an approximately three-fold larger benefit for running compared to walking.

As predicted, we also observed larger $\tau_{sho}$ with added inertia in the hands. $\tau_{sho}$ costs energy via shoulder muscle activation, similar to the elbow, and therefore our results imply that reduced length of the entire forelimb also benefits walking and running. This finding is consistent with a spring-pendulum model of forelimb swing during walking in humans, where the shoulder muscles tune the natural frequency of the forelimb by adjusting the effective stiffness of the shoulder (Yegian et al., prepared). Longer forelimbs require stiffer shoulders, and consequently more muscle torque. Therefore, our results suggest that for a given hindlimb length, longer forelimbs are more costly to swing during bipedal walking. However, the spring-pendulum model suggests that stiffness is a non-linear function of forelimb length (Yegian et al., prepared), suggesting that simple skeletal ratios like the intermembral index (forelimb length divided by hindlimb length) may not be adequate heuristics for comparing walking mechanics across different body sizes.

The experimental manipulation of adding 1.36 kg to the hands is a substantially larger inertial change than any variation in BI observed in hominins, yet the manipulation increased $T_{elb}$ by only 16% in walking and 52% in running. This difference suggests that any BI shift that occurred in hominins had an even smaller proportional effect on elbow mechanics. Although the energetic cost of swinging the forelimbs during walking and running is unknown, estimates
of hindlimb swing cost range between 10-30% of total cost of locomotion in humans and birds (Marsh et al., 2004; Gottschall, 2005; Modica and Kram, 2005; Ellerby and Marsh, 2006; Doke et al., 2007). Forelimb swing cost is likely a smaller portion of the total cost due to smaller torque magnitudes at the shoulder and elbow compared to the hip and knee.

The benefit of a smaller BI in terms of proportional change to instantaneous locomotion cost is likely quite small, yet even very small instantaneous energetic benefits can add up over time and affect selection. For example, the gross daily cost of walking in contemporary Hadza hunter-gatherers is estimated to be on average approximately 291 kCal for men and 126 kCal for women (Pontzer et al., 2015), and the total locomotion cost is greater when running is added to daily activity. If the BI shift that occurred in H. erectus yields a 1% savings in locomotion energy cost, the savings for contemporary hunter-gatherers is in the order of approximately 1-5 kCal each day. Over the course of a year, the incremental savings would add up to roughly 1000 kCal, or several days’ worth of walking energy expenditure. We therefore hypothesize that walking and running, especially for long distances, would have contributed to selection for relatively shorter distal forelimbs in hominins.

**Evolution of Brachial Index in Hominins**

The last common ancestor of chimpanzees and hominins is most likely somewhat chimpanzee-like in terms of morphology and locomotion, although there is ongoing debate on this issue (Gebo, 1996; Richmond et al., 2002b; Thorpe et al., 2007; Lovejoy et al., 2009; Pilbeam and Lieberman 2017). On average, chimpanzees exhibit Bis of approximately 93 (Schultz 1937), while ARA-VP-6/500, the oldest hominin in the dataset used in this study, is
estimated to have a similar BI of 90 (Lovejoy et al., 2009). Estimates for the specimens assigned to *Australopithecus* and *Homo habilis* mostly range from 82 (MH2) to 88 (AL 288-1), with the exception of BOU-VP-12 (98, although this large value may be the result of an underestimated humerus length; Asfaw et al., 1999; Haile-Selassie et al., 2010). If ARA-VP-6/500 approximates ancestral BI, the somewhat smaller values observed in *Australopithecus* and *H. habilis* may reflect an initial shift driven by selection for human-like walking. There is evidence for modern hindlimb and center-of-mass walking mechanics in the Laetoli footprints dated to 3.7 m.y.a., presumably created by australopiths (Raichlen et al., 2008; 2010; Crompton et al., 2012; Dingwall et al., 2013). However, several of the early hominin forelimb bones are only preserved in fragments (particularly AL 288-1, BOU-VP-12, and OH 62) and are prone to large uncertainties in length estimations. With the lack of a clear ancestral BI value to compare to and an uncertain fossil record, evidence for an initial shift driven by walking must be considered weak.

Later fossil specimens assigned to *Homo* tend to have intact or fully reconstructed forelimb long bones, and clearly show a shift to smaller BI values when compared to older specimens with similarly complete long bones (i.e. StW 573 and MH2); later *Homo* species tend to exhibit smaller BI than australopiths by approximately 5 to 15 points (Table 2.1). The timing of the shift coincides with the evolution of the hunter-gatherer lifestyle and associated locomotion patterns, namely long distance walking and endurance running (Bramble and Lieberman, 2004), and when combined with the biomechanical evidence from this study suggests that long distance walking and endurance running drove the shift. Of note, while LB1 shows evolutionary convergence to a body size and limb lengths similar to a small *Au. afarensis*
(AL 288-1), a typical hunter-gatherer Bl of 78 was retained in *Homo floresiensis* (Brown et al., 2004). This observation suggests that the shift in Bl was not driven by scaling effects between the forelimb elements across body size, and implies that the shift was instead driven by selection.

The results of our experiment suggest that the derived, stable range of BIs between 70 and 80 in hominin hunter-gatherers are an adaptation to long distance walking and running. This study provides the first mechanistic explanation for the observed shift in Bl in hominins, and highlights the benefit of using biomechanical experiments with modern humans to predict directional effects of selection on hominin skeletal anatomy. Future research, however is needed to estimate the actual energetic savings associated with forelimb shortening to quantitatively compare performance effects with other activities such as climbing, throwing and tool-making.
References


Raichlen DA, Gordon AD, Harcourt-Smith WEH, Foster AD, Haas WR. 2010. Laetoli Footprints


Chapter 3 - Functional scaling of forelimb swing mechanics during bipedal walking explains the evolution of hominin limb proportions.

Abstract

The evolution of terrestrial bipedalism is a fundamental question in hominin evolution. Australopiths had relatively longer forelimbs than later species in the genus Homo, often interpreted as evidence for a shift in locomotion behavior from a more primitive mixed arboreal/terrestrial strategy in Australopithecus to the economical, near-obligate bipedalism of Homo. However, this interpretation does not take into context how size affects forelimb function during walking. Using the biomechanical Swing Scaling Model that describes forelimb swing mechanics during walking, we illustrate that isometrically scaled modern humans are not functionally similar, as shoulder stiffness controlled by muscles likely increases with increasing size. When limb proportions are scaled to similar shoulder stiffness, all but the earliest hominin limb proportions fall within the Swing Scaling Model prediction. The shift to relatively shorter forelimbs in Homo is mostly explained by an increase in body size, making a transition in locomotion behavior unnecessary to explain the evolution of hominin limb proportions.

Introduction

Adaptations for terrestrial bipedalism evolved early in the hominin lineage as evidenced by late Miocene and early Pliocene fossils (Crompton et al., 2008; Lovejoy et al., 2009c; Zollikofer et al., 2005). The evolutionary pathway to economical, near-obligate terrestrial bipedalism seen in modern humans is complicated by the observation that while many early hominin species, such as australopithecines had features suggesting bipedal locomotion in the
hindlimb, forelimb features tended to be outside the ranges of human variation. This observation has led to the common hypothesis that australopiths represent a tradeoff between terrestrial bipedalism and arboreal locomotion, and longstanding debate as to when human-like bipedalism evolved (Crompton et al., 2008; Crompton et al., 1998; Hunt, 1994; Jungers, 2009; Kramer and Eck, 2000; Lovejoy, 1988; Raichlen et al., 2010; Stern and Susman, 1983; Ward, 2002).

Interlimb proportions serve as a rough indicator of locomotion behavior in extant primates (Fleagle, 2013). Limb proportions are often expressed by the intermembral index (IMI, (humer+radius)/(femur+tibia)*100), which compares the length of the forelimb to the length of the hindlimb. Quadrupedal monkeys are generally constrained to values near 100 (i.e. equal limb lengths), while in hominoids developmental constraints are relaxed allowing for the evolution of large variation in IMI within the family (Young et al., 2010). Apes, which utilize climbing/suspensory behavior to some degree, have IMI>100, while bipedal humans have IMI values ~70 (Schultz, 1937). Within hominins, *Ardipithecus* and *Australopithecus* fossils indicate IMI values above the range of human variation, and modern IMI values do not appear until the advent of large-bodied *Homo erectus* in Africa (Holliday et al., 2018).

Relatively long forelimbs in small-bodied australopithecines, intermediate to apes and humans, are generally interpreted as evidence that the transition to economical near-obligate bipedalism characteristic of modern humans did not occur until the evolution of *Homo* (Hunt, 1994; Jungers, 2009; Stern and Susman, 1983). This interpretation rests on the observation that IMI is independent of size in humans, indicating an isometric scaling relationship between the limbs (Jungers, 2009). While limb lengths scale isometrically within the human species, it does
not necessarily follow that locomotion function and costs also scale isometrically and are similar across the range of human stature. Although developmental constraints governing interlimb proportions are relaxed in hominoids compared to quadrupedal monkeys, there are still strong correlations between limb lengths within species (Young et al., 2010). Therefore, independence between IMI and size in humans may be the result of underlying isometric developmental integration between the limbs within a species rather than similar function during bipedal gait, and scaling of similar function may follow an allometric relationship between forelimb and hindlimb length.

In order to explore whether isometrically scaled human limbs are equivalent in function during bipedal walking, and whether functional scaling can explain some of the variation in hominin IMI, we introduce in this paper a novel biomechanical model of forelimb swing during walking that incorporates the anatomical lengths of both the forelimbs and the hindlimbs. We then use the Swing Scaling Model to test for a relationship between shoulder muscle torque and size within a modern human sample and compare fossil hominin limb lengths to a limb length scaling relationship based on functional similarity.

*Swing Scaling Model*

Forelimb swing during walking in humans serves the function of reducing the total energetic cost of locomotion (Collins et al., 2009; Umberger, 2008). In each stride the forelimbs swing in opposite timing to the movement of the hindlimbs, resulting in opposing angular momenta about the vertical axis passing through the body’s center of mass (Collins et al., 2009; Elftman, 1939; Herr and Popovic, 2008; Li et al., 2001). This counterbalancing mechanism
reduces the change in total angular momentum of the body and reduces the need for leg and trunk muscles to spend energy controlling twisting of the body.

Forelimb swing is driven by mechanical energy derived from the lower body via forced oscillation, which entrains the forelimbs to swing at stride frequency \( f_{\text{stride}} \) (Pontzer et al., 2009). Although the shoulder muscles do not perform net mechanical work for swinging the forelimbs, they produce workless torques an energetic cost (Collins et al., 2009; Elftman, 1939; Goudriaan et al., 2014; Kuhtz-Buschbeck and Jing, 2012) that play a critical role in producing the observed phase relationship between trunk torsion and forelimb swing during walking in humans (Yegian, 2012). From forced oscillation mechanics, the relative phase within the stride of forelimb swing in relation to the forcing motion of the shoulder, which itself is driven by the hindlimbs, is entirely dependent on the frequency ratio \( r_{\text{freq}} \) (Yegian, 2012), which is the ratio of forcing frequency (in the case of forelimb swing, \( f_{\text{stride}} \)) to the natural frequency of the forelimb \( (f_{\text{nat}}) \):

\[
r_{\text{freq}} = \frac{f_{\text{stride}}}{f_{\text{nat}}} \quad \text{Equation 1}
\]

Because \( f_{\text{stride}} \) changes with speed (Bertram, 2005), shoulder muscles must tune \( f_{\text{nat}} \) in order to maintain constant \( r_{\text{freq}} \) and consistent phasing of forelimb swing across all walking speeds. To illustrate the way muscles tune the natural frequency of the forelimb, Yegian modeled forelimb swing as a single pendulum forced by acceleration of the shoulder joint and controlled by a rotational spring in the shoulder which represents muscle activity (Yegian, 2012). The equation for the natural frequency of a passive pendulum (i.e. only gravity acting on the pendulum) is:
with \( g \) the gravitational constant, \( R_G \) the radius of gyration of the forelimb, and \( \beta \) a dimensionless parameter that captures the mass distribution of the limb, defined as the length between the center of mass and shoulder joint divided by \( R_G \). The addition of a spring-like muscle torque at the shoulder adjusts the natural frequency of the pendulum via the stiffness coefficient \( k \) (Nm/rad) (Yegian, 2012):

\[
4_{\text{nat}} = 2\pi e^{-\frac{\beta g}{R_G}} \quad \text{Equation 2}
\]

\[
4_{\text{nat}} = 2\pi e^{-\frac{\beta g}{R_G} + \frac{k}{mR_G^2}} \quad \text{Equation 3}
\]

with \( m \) the mass of the limb. When \( k=0 \), equation 3 simplifies to the typical \( f_{\text{nat}} \) of a passive pendulum. When \( k>0 \), \( f_{\text{nat}} \) is greater than that of a passive pendulum. As \( f_{\text{stride}} \) increases with speed in humans so does \( k \), keeping \( f_{\text{freq}} \) at a constant value slightly less than 1 (Yegian, 2012).

Stiffness is defined as a torque (or force) per unit displacement, so in the case of the spring-pendulum model \( k \) represents the torque created by the shoulder muscles (\( \tau_{\text{musc}}, \text{Nm} \)) per angular displacement of the limb (\( \Delta \theta, \text{rad} \)):

\[
k = \frac{\tau_{\text{musc}}}{\Delta \theta} \quad \text{Equation 4}
\]
In this sense, $k$ does not represent the tissue stiffness of the underlying muscles but rather a linear control function that relates net muscle torque to angular displacement of the forelimb. Because of the well-established relationship between mass-specific joint torque and mass-specific metabolic rate, we use forelimb mass $m$ and equation 4 to define a new parameter $K$ (Nm/rad/kg), which represents a mass-specific control relationship between shoulder torque and swing (or a “mass-specific stiffness” of the shoulder joint) that accounts for differences in torque between different sized individuals:

$$\frac{k}{m} = K \frac{\tau_{musc}}{m \cdot \Delta \theta}$$

Equation 5

Therefore, when individuals have equal values of $K$ they also have equivalent mass-specific shoulder torque per degree of forelimb swing and can be considered functionally equivalent.

To test forelimb swing function across different sizes we also must account for the relationship between size and $f_{\text{stride}}$ in humans. We use the dynamic similarity hypothesis to do so, which posits that individuals have similar locomotion dynamics when they move at the same dimensionless Froude number ($Fr$) (Alexander and Jayes, 1983). Froude number is expressed as:

$$Fr = \frac{v^2}{g \cdot L_{\text{hind}} \cdot a}$$

Equation 6

With $v$ the forward walking speed (m/s) and $L_{\text{hind}}$ a measure of the length of the hindlimb (in this study the sum of femur+tibia length, m). Forward velocity can be broken down into $v = f_{\text{stride}} \cdot L_{\text{stride}}$, with $L_{\text{stride}}$ the length of the stride. Dynamic similarity predicts that individuals of
different sizes use the same dimensionless relative stride length ($\delta$, defined as $L_{\text{stride}} / L_{\text{hind}}$) at a given Froude number (Alexander and Jayes, 1983), so equation 6 can be restated as:

$$Fr \cdot \frac{f_{\text{stride}}^2 \cdot \delta^2 \cdot L_{\text{hind}}}{g}$$

Equation 7

Combining equations 1, 3, 5, and 7 yields the Swing Scaling Model form:

$$\frac{\delta^2 \cdot r_{\text{freq}}^2}{4\pi^2 \cdot g \cdot Fr} \cdot L_{\text{hind}} \cdot \frac{R_G^2}{\beta \cdot g \cdot R_G + K}$$

Equation 8

The Swing Scaling Model relates the kinematics of walking ($\delta$, $r_{\text{freq}}$, $Fr$) to muscle torque at the shoulder (using $K$ as a proxy) across a spectrum of limb length geometry ($L_{\text{hind}}$, $R_G$). When holding all other variables constant (and assuming $\beta g \cdot R_G > K$), the model predicts $K \propto 1/ \delta^2$ and $K \propto 1/ r_{\text{freq}}^2$, such that increases in relative stride length or frequency ratio reduce the need for muscle torque at the shoulder. In contrast, the model predicts that $K \propto L_{\text{hind}}$ when limb proportions are held constant, with greater shoulder muscle torque in larger individuals sharing the same IMI (see Derivation at end of chapter). Similarly, if limb proportions change by increasing $R_G$ for a given $L_{\text{hind}}$ (i.e. larger IMI), then the model predicts $K \propto \text{IMI}$. The Swing Scaling Model illustrates that while relatively shorter forelimbs reduce the need for muscle torque at the shoulder at a given hindlimb length, isometrically scaled individuals have different $K$ values and likely different costs of swinging the limb, and cannot be considered functionally similar.
In this study we utilized two versions of the Swing Scaling Model: an isometric model, which fixed limb proportions to the IMI of modern humans and allowed $K$ to vary, and a constant $K$ model, which fixed $K$ to the mean value in modern humans and allowed limb proportions to vary. The isometric model therefore provides a scaling relationship driven by similar shape as in humans, while the constant $K$ model provides a scaling relationship driven by functional similarity to compare fossil hominin limbs to modern humans.

Methods and Materials

Experimental Data Collection

Walking mechanics were recorded in a sample of fifteen humans (6 female 9 male; age: 24±3 years; mass: 74±13 kg; height: 1.77±0.09 m; $L_{\text{hind}}$: 0.86±0.05 m; IMI=70±2). The experiment was granted prior approval by the Harvard University IRB, and all participants gave informed consent prior to participation. Standing hip height was measured unshod, and hindlimb length $L_{\text{hind}}$, defined as femur+tibia length, was estimated as 95% of standing hip height based on published anthropometric data and casts of human hindlimb bones (Winter, 2009). Treadmill speed was calculated for each individual using $Fr=0.215$ and $L_{\text{hind}}$ using equation 6. Skeletal forelimb length $L_{\text{fore}}$, defined as humerus+radius length, was estimated from external measurements of the participants.

Walking trials were conducted shod on a split-belt treadmill (Bertec Corp., Columbus, OH, USA) for five minutes. Reflective markers were placed on the right acromion, humeral epicondyles, and styloid processes of the ulna and radius, and were tracked during the trials using eight infrared cameras operating at 200Hz (Qualysis Motion Capture Systems, Goteborg,
Sweden). The wrist and elbow joint centers were estimated as the midpoints between the relevant markers, and the shoulder joint center was estimated as 3 (females) or 3.5 cm (males) below the acromion (De Leva, 1996). Kinematic time series were processed in Igor Pro (Wavemetrics, Lake Oswega, OR, USA) using a 10 Hz lowpass filter. Anthropometric tables (De Leva, 1996) and participant metrics were used to estimate the masses of the limb segments and the positions of the centers of mass. A standard inverse dynamics model consisting of two forelimb segments was used to calculate \( \tau_{\text{musc}} \) at the shoulder (Winter, 2009).

The two forelimb segments were then combined into a single pendulum arm by calculating the position of the center-of-mass of the entire forelimb, and then using the position to calculate the angular displacement of the forelimb \( \Delta \theta \). The total rotational inertia about the shoulder joint, \( I \) (kg\( \cdot \)m\(^2\)), was calculated using the segment mass positions and inertial distributions determined from the kinematic time series and anthropometric tables, respectively. \( R_G \) was calculated from \( I \) and the total mass of the limb, \( m \), using the formula:

\[
R_G = \sqrt[3]{\frac{I}{m}} \quad \text{Equation 9}
\]

Shoulder stiffness \( k \) was then determined as the slope of \( \tau_{\text{musc}} \) vs. \( \Delta \theta \), with model parameter \( K \) the ratio \( k/m \). \( r_{\text{freq}} \) was estimated from equations 1 and 3, while \( \delta \) was estimated using treadmill speed, stride frequency, and \( L_{\text{hind}} \).

*Swing Scaling Model*
The Swing Scaling Model is quantitatively expressed in equation 8. Mean values of $\delta$ and $r_{freq}$ from the experimental sample were used for the model under the assumptions that they are independent of size (i.e. $L_{hind}$). We tested these assumptions by running linear regressions of the two variables against $L_{hind}$ in Matlab (Mathworks, Natick, MA, USA), with the hypothesis that each slope=0. We also assumed that IMI is independent of size in humans (Jungers, 2009), and similarly tested the assumption using linear regression of the related measure $L_{fore}/L_{hind}$ (equivalent to IMI/100) vs. $L_{hind}$.

To test our hypotheses, two versions of the forelimb swing model were constructed. The “isometric model” was created by fixing the model’s limb proportions based on the geometry of the human sample (IMI=70) and solving for $K$ across the range of $L_{hind}$. In this way the isometric model illustrates changes in function, measured as $K$, across size in isometric humans. The “constant K model” was created by fixing the value of $K$ to the experimental mean and then solving for $L_{fore}$ across the range of $L_{hind}$. The constant K model allows relative limb proportions to change with size as long as $K$ remains the same, and represents predicted human limb proportions under a scaling relationship constrained to a single value of $K$. In order to produce a rough prediction interval for the geometry of the constant K model we substituted the upper and lower 95% prediction interval limits from the experimental sample $K$ into the model, yielding $L_{fore}$ length curves that approximately represent the limits of limb length combinations that are consistent with modern human forelimb swing mechanics.

We also estimated $K$ values for limb lengths observed in other hominoids, specifically nine fossil hominin specimens and African apes (see next section), and compared the values to the variation in $K$ observed in the human sample. We note that the hominoid $K$ values are not
estimates of the actual values of $K$ during bipedal walking in the specimens, but rather are used to test whether or not modern humans with those limb lengths would yield similar $K$ values as actual modern humans.

Hominin Fossil Limb Lengths

We compiled a dataset of nine fossil hominin limb lengths by obtaining estimates from the literature for four limb bones: humerus, radius, femur, and tibia (Table 3.1). When multiple estimates for a bone were available in the literature we chose those preferred by the authors, or the midpoint when narrow ranges were given. For a few specimens tibia lengths were estimated using femur lengths and an assumed Crural Index (tibia/femur*100) of 83, following previous studies (Haile-Selassie et al., 2010; Holliday et al., 2018; Richmond et al., 2002). There is no known radius associated with the adult Dmanisi *Homo erectus*, so we estimated its length using a Brachial Index (radius/humerus*100) value of 80 taken from its conspecific, KNM-WT-15000.

The radius of AL 288-1 has been estimated to be as short as 174 mm (Richmond et al., 2002) and as long as 215 mm (Asfaw et al., 1999), alongside further estimates of 181 mm (Holliday et al., 2018) and 206 mm (Kimbel et al., 1994). We chose the midpoint of the short and long estimates (195 mm) as the value for this study. OH 62 presents the greatest challenge for estimating limb lengths due to the highly fragmented nature of the femur and tibia. The commonly cited femur length of 280 mm is almost certainly too short (Reno et al., 2005). McHenry used a somewhat longer estimate of 315 mm in his study estimating body mass of fossil specimens (McHenry, 1991), while Haeusler and McHenry speculated a range of lengths
Table 3.1. Fossil and extant hominoid long bone lengths used in this study (meters).

<table>
<thead>
<tr>
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<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>ARA-VP-6/500</td>
<td><em>Ar. ramidus</em></td>
<td>92</td>
<td>0.278</td>
<td>0.250</td>
<td>0.312</td>
<td>0.262</td>
</tr>
<tr>
<td>StW 573</td>
<td><em>Au. africanus</em></td>
<td>85</td>
<td>0.290</td>
<td>0.240</td>
<td>0.335</td>
<td>0.285</td>
</tr>
<tr>
<td>AL 288-1</td>
<td><em>Au. afarensis</em></td>
<td>83</td>
<td>0.237</td>
<td>0.195</td>
<td>0.281</td>
<td>0.241</td>
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<tr>
<td>BOU-VP-12</td>
<td><em>Au. (garhi?)</em></td>
<td>76</td>
<td>0.236</td>
<td>0.231</td>
<td>0.335</td>
<td>0.278*</td>
</tr>
<tr>
<td>MH2/MH4</td>
<td><em>Au. sediba</em></td>
<td>79</td>
<td>0.269</td>
<td>0.226</td>
<td>0.347</td>
<td>0.290*</td>
</tr>
<tr>
<td>OH 62 (tall)</td>
<td><em>H. habilis</em></td>
<td>71</td>
<td>0.264</td>
<td>0.228</td>
<td>0.379</td>
<td>0.315*</td>
</tr>
<tr>
<td>OH 62 (short)</td>
<td><em>H. habilis</em></td>
<td>85</td>
<td>0.264</td>
<td>0.228</td>
<td>0.315</td>
<td>0.261*</td>
</tr>
<tr>
<td>Dminisiadult</td>
<td><em>H. erectus</em></td>
<td>77</td>
<td>0.295</td>
<td>0.236**</td>
<td>0.382</td>
<td>0.306*</td>
</tr>
<tr>
<td>KNM-WT-15000</td>
<td><em>H. erectus</em></td>
<td>71</td>
<td>0.319</td>
<td>0.255</td>
<td>0.432</td>
<td>0.380*</td>
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<tr>
<td>LB1</td>
<td><em>H. floresiensis</em></td>
<td>84</td>
<td>0.243</td>
<td>0.190</td>
<td>0.280</td>
<td>0.235</td>
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<tr>
<td>Pan ♂</td>
<td>107</td>
<td>0.306</td>
<td>0.285</td>
<td>0.300</td>
<td>0.251</td>
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</tr>
<tr>
<td>Pan ♀</td>
<td>106</td>
<td>0.290</td>
<td>0.269</td>
<td>0.286</td>
<td>0.239</td>
<td></td>
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<tr>
<td>Gorilla ♂</td>
<td>117</td>
<td>0.437</td>
<td>0.351</td>
<td>0.376</td>
<td>0.300</td>
<td></td>
</tr>
<tr>
<td>Gorilla ♀</td>
<td>118</td>
<td>0.368</td>
<td>0.294</td>
<td>0.311</td>
<td>0.251</td>
<td></td>
</tr>
</tbody>
</table>

a Lovejoy et al. (2009)
b Heaton et al. (BioRxiv)
c Pontzer et al. (2010)
d midpoint of high and low estimates; see Holliday et al. (2018)
e Richmond et al. (2002)
f MH2 forelimb, MH4 hindlimb adjusted by +7%; Holliday et al. (2018)
g from human regression in Haeusler and McHenry (2004)
h McHenry (1991)
i Morwood et al. (2005)
j Jungers et al. (2009)
* estimated using a crural index of 83
** estimated using a brachial index of 80 taken from KNM-WT-15000
Pan and Gorilla data from Schultz (1937)
centered around 379 mm based on human femurs (Haeusler and McHenry, 2004). Further complicating the hindlimb length estimate is the fact that the tibial length of OH 62 is also unknown and must be estimated using an assumed Crural Index. While some have claimed OH 62 is uninformative due to its fragmented nature (Reno et al., 2005), we chose to include two versions of OH 62 in the dataset using the short and long femur estimates in order to present an approximate range of values that likely contains the actual in vivo length.

We included a representative of Australopithecus sediba in our dataset, consisting of a composite of the forelimb from MH2 and the hindlimb from MH4 following Holliday et al. (Holliday et al., 2018). The authors concluded that MH2 was likely somewhat larger than MH4, with estimates of femoral head diameters suggesting that MH2 was ~7% larger. To account for the size difference between the individuals, the estimates for MH4’s femur and tibia (324 mm and 271 mm, respectively) were adjusted by +7% to the values 347 mm and 290 mm.

African apes (Pan and Gorilla) were included in the comparative dataset using values published by Schultz (Schultz, 1937); average bone lengths for males and females are presented separately in Table 3.1 alongside the hominins.

Results

Experimental Results and Model Tests

Table 3.2 presents the mean values of $L_{fore}$, $L_{hind}$, IMI, $R_G$, $K$, $\delta$, and $r_{freq}$ measured in the experimental sample and used in the isometric and constant $K$ models. Tests of the three model assumptions are illustrated in Figure 3.1. Linear regressions indicated no relationship between $\delta$ and $L_{hind}$ (slope=-0.231, se=0.135, p=0.0813), $r_{freq}$ and $L_{hind}$ (slope=0.059, se=0.207, p=0.7596),
Table 3.2. Geometric and biomechanical values from the experimental human sample.

<table>
<thead>
<tr>
<th></th>
<th>$L_{\text{fore}}$ (m)</th>
<th>$L_{\text{hind}}$ (m)</th>
<th>IMI</th>
<th>$R_G$ (m)</th>
<th>$\beta$ (Nm/rad/kg)</th>
<th>$K$</th>
<th>$\delta$</th>
<th>$r_{\text{freq}}$</th>
</tr>
</thead>
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<tr>
<td>mean</td>
<td>0.601</td>
<td>0.857</td>
<td>70.2</td>
<td>0.340</td>
<td>0.813</td>
<td>1.492</td>
<td>1.663</td>
<td>0.981</td>
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<tr>
<td>s.d.</td>
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<td>0.049</td>
<td>2.3</td>
<td>0.021</td>
<td>0.003</td>
<td>0.282</td>
<td>0.024</td>
<td>0.033</td>
</tr>
<tr>
<td>s.e.m.</td>
<td>0.009</td>
<td>0.013</td>
<td>0.6</td>
<td>0.005</td>
<td>0.001</td>
<td>0.073</td>
<td>0.006</td>
<td>0.009</td>
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</tbody>
</table>
Figure 3.1 Test of forelimb swing model assumptions. Three variables are assumed to be independent of size and are treated as constants in the forelimb swing model: relative stride length (squares), frequency ratio (triangles), and relative limb proportions (diamonds). Solid lines are averages of the fifteen experiment participants. Linear regression indicated no relationship between any of the variables and hindlimb length.
and $L_{\text{fore}}/L_{\text{hind}}$ and $L_{\text{hind}}$ (slope=-0.086, se=0.143, p=0.5182), validating the assumptions that these variables are independent of size.

Model predictions under the assumption of isometric limb scaling were tested via linear regression in the human sample and are presented in Table 3.3 and Figure 3.2. The isometric model predicted inverse relationships for $K$ v. $\delta^2$ and $K$ v. $r^2_{\text{freq}}$, which were supported by significant negative coefficients for $\delta^2$ (slope=-1.551, se=0.308, p=0.0005, Figure 3.2A) as well as $r^2_{\text{freq}}$ (slope=-3.670, se=0.361, p<0.0001, Figure 3.2B) in the regression. The model also predicted positive relationships for $K$ v. $L_{\text{hind}}$ and $K$ v. IMI, similarly supported by regression: $K$ increased with both $L_{\text{hind}}$ (slope=2.161, se=0.482, p=0.0012, Figure 3.2C) and IMI (slope=0.077, se=0.010, p<0.0001, Figure 3.2D) within the experimental sample.

Comparison of Hominoid Limbs to Model Predictions

The positive relationship between $K$ and $L_{\text{hind}}$ in the isometric model is plotted in Figure 3.3, alongside the constant $K$ model fixed to the experimental mean value of 1.492 Nm/rad/kg. The 95% prediction interval for the human sample extended between $K=0.94$ and $K=2.04$. $K$ values calculated using hominin limb lengths mostly fell within the prediction interval for modern humans, with three exceptions (ARA-VP-6/500, Stw 573, and the short-femur version of OH 62). The remaining hominin specimens fell within one standard deviation of the experimental mean, including nearly the entire range of OH 62. In general, $K$ values using hominin limbs followed the predicted trajectory of functional scaling illustrated by the constant $K$ model and fell outside of the prediction from the isometric model. Functional scaling was particularly predictive for the genus *Homo* across a wide range of hindlimb size; for example,
Table 3.3. Linear regression of experimental $K$ values using multiple predictors.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Slope</th>
<th>SE</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>[intercept]</td>
<td>2.090</td>
<td>1.329</td>
<td>0.1467</td>
</tr>
<tr>
<td>$\delta^2$</td>
<td>-1.551</td>
<td>0.308</td>
<td><strong>0.0005</strong></td>
</tr>
<tr>
<td>$r^2_{freq}$</td>
<td>-3.670</td>
<td>0.361</td>
<td><strong>&lt;0.0001</strong></td>
</tr>
<tr>
<td>$L_{hind}$</td>
<td>2.161</td>
<td>0.482</td>
<td><strong>0.0012</strong></td>
</tr>
<tr>
<td>IMI</td>
<td>0.077</td>
<td>0.010</td>
<td><strong>&lt;0.0001</strong></td>
</tr>
</tbody>
</table>

model adj. $R^2$: 0.881
Figure 3.2 Partial residuals of $K$ from linear regression using multiple predictors. All four predictors had statistically significant effects on model parameter $K$ (see Table 3.3), which serves as a proxy for muscle activity. Open circles are individuals from the experimental sample, and solid lines illustrate slopes from the regression model. $K$ was inversely related to the squares of relative stride length (A) and frequency ratio (B), while positively related to hindlimb length (C) and IMI (D) in the sample.
Figure 3.3 K values from the forelimb swing models and calculated using hominoid limb lengths. The left axis indicates the values of $K$, while the right axis indicates the number of standard deviations (z-scores) away from the mean value of $K$. The lines represent solutions for the isometric model, which has the limb proportions of an average human, and the constant $K$ model, which has variable limb proportions and $K$ fixed to the experimental mean. The shaded grey region around the constant $K$ model represents the 95% prediction interval for the human sample (+/- 1.96 z-scores), while dotted lines indicate the interval for the isometric model. $K$ values for the humans were measured during walking, while hominin and ape estimates represent values for hypothetical humans with the given hominoid limb lengths. Two estimates for OH 62 are shown and illustrate a rough range of possible values, given the wide discrepancy in estimated femur length for the specimen.
the value derived for LB 1 (*Homo floresiensis*), the shortest hominin in the dataset, was within 0.9 standard deviations of the human mean.

The two oldest hominin specimens lay above the constant $K$ prediction interval; StW 573 (*Australopithecus africanus*) yielded a $K$ value about 50% greater than and 2.6 standard deviations above the constant $K$ model, while ARA-VP-6/500 (*Ardipithecus ramidus*) yielded a value about 75% greater than and 4 standard deviations above the model. StW 573 was closer to the human range than values for the African apes, while ARA-VP-6/500 was approximately in between: *Pan* limb lengths yielded $K$ values about 150% greater than and 8 standard deviations above the human mean, with *Gorilla* values even farther from the human range.

The interlimb proportions of the isometric and constant $K$ models are contrasted in Figure 3.4, which plots the IMI for each model against $L_{hind}$. Holding $K$ constant resulted in a negative allometric relationship between IMI and $L_{hind}$, with larger hindlimbs linked to smaller IMI values. Functional scaling was a predictor of hominin IMI, with most specimens falling within +/- 4 points of the prediction. In contrast, almost all hominin samples fall above the 95% prediction range of IMI from the human sample. As noted above in the $K$ value results, StW 573 and ARA-VP-6/500 were the exceptions that fell above the constant $K$ prediction interval and were not explained by functional scaling of human bipedal walking, while almost the entire range of OH 62 estimates fell within the prediction interval.

**Discussion**

We investigated two possible limb length scaling relationships using the bipedal Swing Scaling Model: isometric scaling with constant interlimb proportions, and functional scaling
Figure 3.4 Intermembral indices of the forelimb swing models and hominoids. The data are presented in similar form to Figure 3, but with individual fossils denoted by unique symbols. The shaded region surrounding the constant $K$ model is an approximate 95% prediction interval derived by using the upper and lower limits of $K$ illustrated in Figure 3, while the dotted lines enclose the interval for the isometric model.
with constant $K$ when walking. Experimental data collected from modern humans indicated that isometric scaling of the limbs yields a relationship between $K$ and size measured by hindlimb length, with larger individuals requiring larger $K$ values and presumably greater cost of swing (Figures 3.2 and 3.3). In contrast, functional scaling yields a change in limb proportions across size, with larger individuals requiring relatively shorter forelimbs in order to produce the same forelimb swing mechanics as smaller individuals (Figure 3.4).

Our results shed new light on the origins of the genus *Homo* and the evolution of modern limb proportions in the Pleistocene. The emergence of *Homo* coincided with smaller IMI values compared to *Australopithecus*, exemplified by the human-like IMI of *Homo erectus*. The appearance of modern limb proportions in *H. erectus* has previously been thought to represent a transition from mixed locomotion behavior in *Australopithecus*, including climbing/suspension, to near-obligate terrestrial bipedalism in *Homo* (Fleagle, 2013; Hunt, 1994; Jungers, 2009; Stern and Susman, 1983). The observed shift to smaller IMI also coincided with a shift towards larger body size, and the evolution of endurance running and the hunter-gatherer way of life (Bramble and Lieberman, 2004). The results of this study indicate that functional scaling of human bipedal walking mechanics explains most of the IMI shift from *Australopithecus* to *Homo*, suggesting that the relatively short forelimbs of *H. erectus* were driven by the evolution of longer hindlimbs and larger body sizes compared to Pliocene hominins rather than a transition in locomotion behavior.

*Homo floresiensis* provides an evolutionary test case for the hypothesis that the modern IMI observed in *Homo* was driven by evolution of body size rather than a transition in locomotion behavior. *H. floresiensis* was a very short-statured and very recent species found on
the island of Flores in Indonesia (Brown et al., 2004), which likely descended from a large-bodied *H. erectus* population (Kaiu et al., 2011; Kubo et al., 2013) yet had similar IMI as a short-statured *Australopithecus afarensis* (Lucy, AL 288-1). There is ongoing debate as to whether australopith-like features in *H. floresiensis*, such as the IMI of LB1, are symplesiomorphs retained from an early *Homo* ancestor that underwent a previously unknown migration out of Africa (Argue et al., 2017; Jungers et al., 2016), or evolutionary convergence. The results of this study suggest that the australopith-like IMI of *H. floresiensis* and the human like IMI of *H. erectus* lie along the same functional scaling relationship shared with modern humans; just as a shift from the large IMI of Lucy (83) to the human value in KNM-WT-15000 (71) can be linked to the shift to large body size, a shift back to an ancestral IMI in LB1 (84) can be linked to a reversal to small body size. Therefore, the limb proportions of *H. floresiensis* are most simply explained by a *H. erectus* ancestor that converged on the limb proportions of Lucy due to functional scaling of bipedal forelimb swing mechanics.

The fossil specimens assigned to *Australopithecus* and *Ardipithecus* that were used in this study tend to be more fragmentary than the *Homo* specimens (excluding OH 62), with more uncertainty in their IMI estimates. Three australopiths fell within the prediction interval of the Swing Scaling Model using the limb estimates in Table 3.1, while the most complete australopith postcranium (StW 573, *Au. africanus*) lay above the prediction interval. These results suggest that the forelimb swing mechanics of *Au. afarensis* (Lucy), *Au. garhi* (BOU-VP-12/1), and *Au. sediba* (MH2/MH4 composite) were comparable to modern humans, and that *Au. africanus* likely had somewhat greater muscle activation at the shoulder. In general, comparisons of the hominins to the model prediction shows that the relationship between size
and IMI must be accounted for when interpreting forelimb length as a signal of locomotion behavior in fossils. The postcranial anatomy of *Ardipithecus ramidus* (ARA-VP-6/500) contains multiple lines of evidence pointing to a walking gait unlike modern humans (Lovejoy et al., 2009a; Lovejoy et al., 2009c; Suwa et al., 2009), making it unsurprising that the $K$ value and IMI for this specimen lay the furthest away from the human prediction interval. *Ardipithecus* is likely the best example of a mixed locomotion strategy in hominins (Lovejoy et al., 2009b; White et al., 2009), with the evolution of a more modern walking gait in *Australopithecus*. The Laetoli footprints, dated to 3.6 million years ago, provide some evidence that human-like walking was present in the middle Pliocene australopiths (Raichlen et al., 2010; Raichlen et al., 2008), which is further supported in this study by the human-like $K$ estimated for Lucy (3.2 m.y.a.)

Precise comparisons of estimated shoulder muscle torque were limited by the use of $K$ as a proxy. Doing so assumed that the ratio $PCSA \times d_{\text{musc}} / m$ was constant across all individuals, which is likely true on average in isometrically scaled humans. However, interspecific variation in musculotendon anatomy and forelimb mass may cause error when using $K$ as the compared variable. Therefore, this study should be considered a first order comparison, with further estimations of fossil shoulder anatomy and limb mass distribution necessary for more precise estimates of muscle torque.

Intriguingly, the Swing Scaling Model may also shed light on bipedal theropod dinosaur limb scaling. A recent study comparing $L_{\text{fore}}$ and $L_{\text{hind}}$ to snout-vent length ($SVL$) in non-avian theropods yielded the scaling relationships $L_{\text{fore}} \propto SVL^{0.70}$ and $L_{\text{hind}} \propto SVL^{0.88}$ (Dececchi and Larsson, 2013), which suggests that $L_{\text{fore}} \propto L_{\text{hind}}^{0.80}$. Although forelimb function during bipedal locomotion
in dinosaurs has not been explored before, and the forelimbs may have had no function during bipedal gait, if muscle torque at the shoulder was a relevant component of the cost of locomotion the same principles that contributed to negative allometry in hominin limb scaling may have also contributed to negative allometry in non-avian theropod limb scaling.

We used the Swing Scaling Model to investigate forelimb swing during walking in hominins in this study, but the model equation describes the dynamics of a forced pendulum in general, and therefore may be applicable to hindlimb swing. Hip torque during hindlimb swing has previously been approximated as spring-like in a passive dynamic walking model (Kuo, 2001), analogous to the spring-like torque in the shoulder in this study. It has long been known that animals with distally distributed hindlimb mass (i.e. long hindlimb $R_G$ during swing), such as non-cursorial species, take longer relative strides compared to animals with the mass concentrated towards the hip (Alexander and Jayes, 1983; Raichlen et al., 2013). The Swing Scaling Model shows that while longer $R_G$ increases $K$ at the joint (e.g. $K \propto IMI$ in Figure 3.2D), longer relative strides can offset the increase to an extent (e.g. $K \propto 1/ \delta^2$ in Figure 3.2A). Therefore, longer relative strides in non-cursorial animals may be due to conservation of swing cost across a diverse phylogeny.

Conclusions

Although human limb proportions scale isometrically, with constant IMI across all body sizes (Figure 3.1), muscle torque at the shoulder increases with increasing hindlimb length (Figures 3.2 and 3.3). Humans are therefore not functionally similar when it comes to forelimb swing mechanics during walking, and the isometric relationship between limb lengths may be
linked to developmental integration rather than equivalent function. In contrast, interspecific comparisons of hominin limb proportions to a functional scaling prediction suggest that most species of *Australopithecus* and all species of *Homo* had forelimb swing mechanics consistent with the variation observed in modern humans (Figure 3.4). The results of this study provide further evidence that human-like walking evolved in early Australopithecus in the Pliocene, and that the relatively short forearms characteristic of most *Homo* species were a consequence of larger body size rather than a transition in locomotion behavior.

**Derivation**

If limb proportions are fixed to a constant value (i.e. $R_G / L_{hind} = a$) as in fixed IMI, substituting $a^*$ $L_{hind}$ for $R_G$ in equation 8 and simplifying yields:

$$
\frac{\delta^2 \cdot r_{freq}^2}{4\pi^2 \cdot g \cdot Fr} \cdot \frac{a^2 \cdot L_{hind}}{\hat{\beta} \cdot g \cdot a \cdot L_{hind} + K}
$$

Therefore $K$ is positively related to $L_{hind}$ (when all other variables are held constant), specifically they vary in direct proportion.
References


Conclusions

The first three chapters of this thesis directly tested hypotheses about how anatomy affects function during bipedal locomotion in order to better understand the evolution of hominin forelimbs, focusing on the length of the distal segment and the overall length as the relevant anatomical characters. In summary, I found that distal forelimb length affects bipedal gait via elbow mechanics, with longer distal forelimbs increasing elbow muscle torque and presumably the cost of forelimb swing during walking and running. Notably, the effect on elbow torque is more pronounced in running compared to walking, by about three-fold. Overall forelimb length also affects function, as longer limbs increase shoulder muscle torque in modern humans. However, a human-based mechanical model shows that almost all of the hominins, including all australopiths, had forelimb and hindlimb lengths that are consistent with modern human walking dynamics. In the context of bipedalism, the shift to shorter distal forelimbs and shorter relative forelimbs in *Homo erectus* can be explained by the evolution of endurance running and long hindlimbs respectively.

Whether or not tradeoffs existed in the forelimb between bipedalism and other behaviors like climbing remains unknown, and selection for non-locomotion tasks such as tool making may have also played a role in the length shifts observed in the fossil record. In order to test hypotheses about tradeoffs with bipedalism, climbing and tool making will need to be described in a similar mechanical framework as bipedalism in this thesis. Climbing, tool making, throwing, etc. can all be considered skilled tasks, with an optimal set of dynamics that can be learned. Experience or skill at the relevant task must be a critical consideration when designing experiments on biomechanics of human movement to test hypotheses about human evolution.
Implications for Understanding Hominin Evolution

To date, the standard story of hominin evolution is that an intermediate form of bipedal walking evolved in *Ardipithecus* and *Australopithecus*, with the final form of bipedal walking and running evolving in the genus *Homo*. This dissertation challenges the standard story by showing that major changes to the hominin forelimbs, namely the decrease in relative distal forelimb length and the decrease in relative forelimb length overall, can be explained mostly by the evolution of endurance running and larger body size in the genus *Homo*.

In light of the results presented here, I argue for a new paradigm when viewing the evolution of hominins and the fossil record: that human-like walking evolved early on by the time of *Australopithecus*, with endurance running added as an ecologically relevant gait with the advent of *Homo erectus*. The previous analytic approach of comparing fossil hominin specimens to chimpanzees and humans and using analogy to interpret extinct gait has flaws when function cannot be so easily interpolated from the geometry of fossil bones. Rather, a functional approach that uses biomechanical modeling to assess how variation found in the fossil record would affect the costs of bipedal walking and running is the most fruitful approach to understanding hominin locomotion behavior going forward.