

Why Lucy didn't go far or fast

Abstract

This review aims to examine the running abilities of *Australopithecus afarensis* in an evolutionary context. Fossil and biomechanical evidence indicate that while *A. afarensis* was capable of bipedal walking and limited running, it lacked the specialized adaptations for endurance running found in later Homo species. These findings suggest that environmental changes and mosaic habitats shaped the gradual evolution of human locomotion, highlighting *A. afarensis* as a transitional form between arboreal and fully terrestrial hominins.

Introduction

The evolution of human locomotion is a key concept in the field of palaeoanthropology. Bipedal gait, a unique adaptive trait of hominins, is evident in the fossils of many early hominin species. A significant example is Lucy (AL 288-1), a 3.2-million-year-old *Australopithecus afarensis* fossil discovered in Hadar, Ethiopia (Johanson & Gray, 1974). With a nearly complete skeleton (40%) and 47 of its bones preserved, Lucy was the oldest and most complete fossil discovered at the time.

In addition to Lucy, other important discoveries have contributed to the understanding of early hominin bipedalism. These include the earlier found *Australopithecus africanus* fossil of the Taung child (Dart & Salmons, 1925), thirteen fossils of *A. afarensis* discovered shortly after Lucy (Bush, 1978), and the Laetoli footprints attributed to *A. afarensis* (Leakey & Hay, 1979). These key fossils, along with later discoveries show several key features that support the evidence of bipedalism, such as a downward-oriented foramen magnum, spinal curvature, a low and wide pelvis, an inward thigh angle, a straight tibia, a higher rib curvature, a forward-oriented hallux, and the latter discovery of the metatarsal (Dart and Salmons, 1925; Johanson and Gray, 1974; Bush, 1978; Leakey & Hay, 1979; Ward et al., 2011).

Bipedal locomotion in modern humans consists of two gaits, walking and running. Although extensive studies have been done on early hominin walking, substantially less research has focused on early running performance and its evolutionary significance.

Running consists of two forms, sprinting and endurance running. Sprinting is running at maximal speed over a short distance and endurance running (ER) is the continuous running over long distances through extended time periods using aerobic metabolism. Humans are poor sprinters compared to most cursorial mammals but excellent endurance runners showing average speeds of $3.2\text{--}4.2\text{ms}^{-1}$ (Cavanagh & Cram, 1989). ER is also unique to humans among primates and most mammals.

Walking and running, although seemingly similar have two completely different biomechanics. Walking shows an inverted pendulum biomechanism, where during stance phase the stance foot is fixed in place with the centre of mass showing an oscillatory motion around it. An efficient exchange between potential and kinetic energy is the driving force for this motion, resulting in low energy expenditure. Running however shows a mass spring model, similar to the oscillatory motion of a mass attached to a spring. Here, energy is stored in collagen rich ligaments and tendons in the form of elastic strain energy during contact/ stance phase and released through a recoil mechanism during toe off/ propulsive phase (Ker et al., 1987). Due to the difference in mechanisms each gait requires completely different structural modifications.

Structural evidence for endurance running will be discussed under four demands as cited by Bramble and Lieberman (2004), energetics, skeletal strength, stabilization, and thermoregulation.

This review aims to discuss structural evidences of running in *Australopithecus afarensis* and to understand its evolutionary implications.

Methodology

Literature survey of over twelve research articles through google scholar database, using keywords such as “Lucy”, “running performance”, “endurance running”, “evolution of human running”, and “*Australopithecus afarensis*”.

Results

Energetics

During running elastic strain energy is stored by ligaments and tendons in compliant leg at heel strike and released through recoil during toe off (Ker et al., 1987). In order to economically generate energy for transport comparative to ape like ancestors, latter hominins have developed long, spring-like ligaments and tendons. Achilles tendon, which connects the calcaneus to the major plantar flexor is fundamental for running. Although no fossilized remains of soft tissues are found, a study on calcaneus bones of three *A. afarensis* specimens in Hadar showed a posterior narrower attachment surface of achilles tendon similar to modern chimpanzee (Latimer & Lovejoy, 1989). Another study which measured the steady state running performances of two Lucy models using achilles tendon and muscle architectures of ape and human, showed gait measurements of slow steady state running even when tricep surae mass and achilles tendon was reduced to ape like size. Lower speeds (1.74 – 4.97 ms⁻¹) and higher cost of transport (x1.7 – 2.9) was observed (Bates et al., 2025).

The foot arches, both transverse and longitudinal, play a crucial role in bipedal running. Longitudinal arch in particular aids in both maintaining foot rigidity and storing elastic strain energy. Partial plantar arch seen in Hadar and Sterkfontein specimens aid in maintaining midtarsal rigidity and function in storing and releasing elastic strain energy (Aiello & Dean, 1990). Another study on radiographs of tibial arch angles (TAA) and its relatedness to rearfoot arching, done on Lucy and two other specimens from Hadar, showed asymptomatic flatfootedness (lower longitudinal arch) in Lucy, but not in the two other specimens (DeSilva & Throckmorton, 2010). This suggested possible variations among the species with some accounts of rearfoot arching.

Stride length which is the length travelled by both feet during a single gait cycle is essential in improving endurance running efficiency as running speeds can be increased by increasing stride length while keeping stride rate at a constant. Limb length is essential for maintaining longer stride lengths, however lower leg length (~50% less than *Homo erectus*) seen in *A. afarensis* suggest lower stride length and speed (Aiello & Dean, 1990).

Skeletal strength

High skeletal stress is important during running in order to withstand vertical ground reaction forces which at its peak can reach up to $\times 3-4$ that of body weight. This is overcome by adaptations such as expanded joints with larger articulation area to lower joint stress. However smaller joints in *A. afarensis* compared to *Homo erectus* suggest lower skeletal strength. Another study estimated limb bone safety factor level (bone strength during high performance activities) of femur midshaft model of Lucy using bone stress experiments to be 5-6 which was much higher compared to 2-4 seen in most cursorial vertebrates (Bates et al., 2025). As suggested by the author these values may be due an error in model or lack of consideration of other factors such as limb musculature and body proportions.

Stabilization

Bipedal gaits are inherently unsteady, requiring special mechanisms for balance and stabilization. Independent and isolated rotation of the trunk relative to hip, due to the separation of thorax from pelvis by the waist aids in maintaining balance while running. Waist is present, however wider in *A. afarensis* due to broader shoulders, rib cage and pelvis, suggesting lower balance when running. In addition during leg acceleration destabilizing torques are created, and are counteracted by opposed torques of thorax and arm counter rotation. This ability is also hindered in *A. afarensis* by the presence of broad shoulders and large neck and head muscles (Stern Jr. & Susman, 1983).

Another study on the contribution of transverse arch to midfoot stiffness, showed that it had an amplifying effect on the intrinsic stiffness of foot unlike the longitudinal arch. A formula for stiffness with respect to normalized curvature was formulated and observed to be below human range in *A. afarensis* (Al-333, and Laetoli footprints) (Venkadesan et al., 2020).

Discussion

The locomotor abilities of *Australopithecus afarensis*, exemplified by the Lucy specimen, provide critical insight into the evolutionary trajectory from arboreal ape-like ancestors to the endurance running capabilities of modern humans. Recent biomechanical simulations and fossil analyses confirm that while *A. afarensis* was mechanically capable of bipedal running, its absolute and size-normalized maximum speeds were substantially lower than those of *Homo sapiens* and later hominins. This limited running performance aligns with anatomical evidence indicating a mix of arboreal and terrestrial adaptations, including a relatively short lower limb, broad pelvis, and features favourable for both climbing and upright locomotion.

The evolutionary significance of these findings is emphasized by the endurance running hypothesis, that the anatomical and physiological adaptations for long-distance running are unique to the genus *Homo* and played a pivotal role in enabling persistence hunting and efficient scavenging in open environments (Bramble, D. M., & Lieberman). In contrast, *A. afarensis* lacked several key adaptations for endurance running, such as elongated lower limbs, robust Achilles tendons, and fully developed foot arches, which only appear in later hominins. The relatively low cost of transport observed in *A. afarensis* was comparable to mammals and birds of similar body size, but the limited speed range and absence of specialized running features suggest that endurance running was not a primary selective pressure during its evolutionary period.

Environmental changes during the late Miocene and Pliocene epochs, particularly the transition from dense forests to more open woodland and savanna habitats, exerted selective pressures on early hominins for improved terrestrial locomotion. The Savannah Hypothesis and related models propose that as African landscapes became more open and fragmented, bipedalism provided several adaptive advantages, including efficient locomotion across greater distances, thermoregulation, and the ability to carry food or tools (Senut et al., 2018). However, the persistence of arboreal traits in *A. afarensis* indicates that these hominins inhabited a mosaic environment, requiring both terrestrial and climbing abilities for survival.

In conclusion, *Australopithecus afarensis* likely occupied an intermediate evolutionary position, capable of upright walking and limited running but lacking the specialized adaptations for endurance running to the extent seen in genus *Homo*. Understanding of biomechanics and its unique structural adaptations also suggest that rather than evolution as a byproduct of enhanced walking, it evolved independently to fulfill selective pressures posed by its unique environment.

References

- Aiello, L., & Dean, C. (1990). An introduction to human evolutionary anatomy. Academic Press.
- Bates, K. T., McCormack, S., Donald, E., Coatham, S., Brassey, C. A., Charles, J., ... & Sellers, W. I. (2025). Running performance in *Australopithecus afarensis*. *Current Biology*, 35(1), 224–230.
- Bramble, D. M., & Lieberman, D. E. (2004). Endurance running and the evolution of *Homo*. *Nature*, 432(7015), 345–352.
- Cavanagh, P. R., & Kram, R. (1989). Stride length in distance running: velocity, body dimensions, and added mass effects. *Med Sci Sports Exerc*, 21(4), 467-79.
- Dart, R. A., & Salmons, A. (1925). *Australopithecus africanus*: the man-ape of South Africa. *A Century of Nature: Twenty-One Discoveries that Changed Science and the World*, 10-20.
- DeSilva, J. M., & Throckmorton, Z. J. (2010). Lucy's flat feet: the relationship between the ankle and rearfoot arching in early hominins. *PLoS One*, 5(12), e14432.
- Ker, R. F., Bennett, M. B., Bibby, S. R., Kester, R. C., & Alexander, R. M. (1987). The spring in the arch of the human foot. *Nature*, 325(6100), 147-149.
- Latimer, B., & Lovejoy, C. O. (1989). The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *American Journal of Physical Anthropology*, 78(3), 369-386.
- Leakey, M., & Hay, R. (1979). Pliocene footprints in the Laetoli beds at Laetoli, northern Tanzania [Review of Pliocene footprints in the Laetoli beds at Laetoli, northern Tanzania]. *Nature*.

Senut, B., Pickford, M., Gommery, D., & Ségalen, L. (2018). Palaeoenvironments and the origin of hominid bipedalism. *Historical Biology*, 30(1-2), 284-296.

Stern Jr, J. T., & Susman, R. L. (1983). The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology*, 60(3), 279-317.

Venkadesan, M., Yawar, A., Eng, C. M., Dias, M. A., Singh, D. K., Tommasini, S. M., ... & Mandre, S. (2020). Stiffness of the human foot and evolution of the transverse arch. *Nature*, 579(7797), 97–100.

Ward, C. V., Kimbel, W. H., & Johanson, D. C. (2011). Complete fourth metatarsal and arches in the foot of *Australopithecus afarensis*. *Science*, 331(6018), 750-753.