Endurance running and the evolution of *Homo*

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Striding bipedalism is a key derived behaviour of hominids that possibly originated soon after the divergence of the chimpanzee and human lineages. Although bipedal gaits include walking and running, running is generally considered to have played no major role in human evolution because humans, like apes, are poor sprinters compared to most quadrupeds. Here we assess how well humans perform at sustained long-distance running, and review the physiological and anatomical bases of endurance running capabilities in humans and other mammals. Judged by several criteria, humans perform remarkably well at endurance running, thanks to a diverse array of features, many of which leave traces in the skeleton. The fossil evidence of these features suggests that endurance running is a derived capability of the genus *Homo*, originating about 2 million years ago, and may have been instrumental in the evolution of the human body form.

Most research on the evolution of human locomotion has focused on walking. There are a few indications that the earliest-known hominids were bipeds[1,2], and there is abundant fossil evidence that australopithecines habitually walked by at least 4.4 million years (Myr) ago[3,4]. Many researchers interpret the evolution of an essentially modern human-like body shape, first apparent in early *Homo erectus*, as evidence for improved walking performance in more open habitats that came at the expense of retained adaptations in the australopithecine postcranium for arboreal locomotion (for example, refs 5–8). Although the biomechanics of running, the other human gait, is well studied, only a few researchers (see refs 9, 10 for example) have considered whether running was a mode of locomotion that influenced human evolution. This lack of attention is largely because humans are mediocre runners in several respects. Even elite human sprinters are comparatively slow, capable of sustaining maximum speeds of only $10.2 \, \mathrm{m \, s^{-1}}$ for less than 15 s. In contrast, mammalian cursorial specialists such as horses, greyhounds and pronghorn antelopes can maintain maximum galloping speeds of $15–20 \, \mathrm{m \, s^{-1}}$ for several minutes[11]. Moreover, running is more costly for humans than for most mammals, demanding roughly twice as much metabolic energy per distance travelled than is typical for a mammal of equal body mass[12]. Finally, human runners are less manoeuvrable and lack many structural modifications characteristic of most quadrupedal cursors such as elongate digitigrade feet and short proximal limb segments.

However, although humans are comparatively poor sprinters, they also engage in a different type of running, endurance running (ER), defined as running many kilometres over extended time periods using aerobic metabolism. Although not extensively studied in non-humans, ER is unique to humans among primates, and uncommon among quadrupedal mammals other than social carnivores (such as dogs and hyenas) and migratory ungulates (such as wildebeest and horses)[13,14]. Here, we review the evidence for and impact of ER in human evolution. We begin with a discussion of the mechanical differences between walking and running, and how well humans perform at ER compared to other mammals. We then review what is known about the key structural specializations thought to underlie human ER capabilities, the extent to which they may be features that evolved originally for bipedal walking, and the evidence for their appearance in the hominid fossil record. We conclude by outlining some hypotheses for why ER capabilities initially arose in the genus *Homo*, and the significance of this behaviour for human evolution.

How well do humans run long distances?

In considering human running, it helps to start from the perspective of the basic biomechanical differences that distinguish running and walking gaits in all mammals, including human bipeds. These differences are well characterized. Walking uses an 'inverted pendulum' in which the centre of mass vaults over a relatively extended leg during the stance phase, efficiently exchanging potential and kinetic energy out-of-phase with every step (Fig. 1a, b). The metabolic cost of transport (COT) for human walking, like that of other mammals, is a 'U'-shaped curve, in which optimal speed, approximately $1.3 \, \mathrm{m \, s^{-1}}$, is largely a function of leg length[15]. Most humans voluntarily switch to running at approximately $2.3–2.5 \, \mathrm{m \, s^{-1}}$, which corresponds closely to the intersection of the COT curves for walking and running in humans (Fig. 2b)[16,17]. At these higher speeds running becomes less costly than walking by exploiting a mass-spring mechanism that exchanges kinetic and potential energy very differently (Fig. 1b). Collagen-rich tendons and ligaments in the leg store elastic strain energy during the initial, braking part of the support phase, and then release the energy through recoil during the subsequent propulsive phase[18,19]. To use these springs effectively, the legs flex more in running than in walking: flexing and then extending at the knee and ankle during the support phase (Fig. 1a). Limb stiffness relative to body mass in running humans is similar to that of other mammalian cursors[20].

Although extensive data on endurance capabilities are not available for most quadrupedal mammals, several lines of evidence indicate that humans, using criteria such as speed and sustainable distance, are much better endurance runners than has generally been appreciated. Human ER speeds range from approximately 2.3 to as much as $6.5 \, \mathrm{m \, s^{-1}}$ in elite athletes. Average ER speeds for recreational joggers range between $3.2–4.2 \, \mathrm{m \, s^{-1}}$ (ref. 21). From an evolutionary perspective, it is important to note that human ER speeds are exceptional compared to non-human primates. Apes such as chimpanzees, and other primates, such as patas monkeys, can sprint rapidly, but they do so rarely and only for short distances[22,23]. No primates other than humans are capable of ER.

Quadrupedal cursors easily sprint faster than humans over short distances, but sustainable ER speeds of humans are surprisingly comparable to specialized mammalian cursors such as dogs and horses in two respects. The first comparison to make is with trotting, because bipeds are incapable of galloping, but also because human bipedal running and quadrupedal trotting are biomechanically most comparable. Both gaits synchronize contralateral fore- and hindlimbs, effectively restricting each stride cycle to just two steps, and both are inherently 'bouncy' gaits with substantial vertical displacements of the centre of mass[18,24]. When compared

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to quadrupedal trotting, human ER speeds are relatively high when adjusted for body mass (Fig. 2a). The predicted preferred trotting speed for a human-sized (65 kg) quadruped is approximately $2.8 \, m \, s^{-1}$, and the trot–gallop transition is $3.8 \, m \, s^{-1}$ (ref. 25). A more extreme comparison of performance that is not adjusted for body size is between humans and large mammals such as ponies and horses (Fig. 2a). Human ER speeds exceed the preferred trotting $(3.1 \, m \, s^{-1})$ and the trot–gallop transition $(4.4 \, m \, s^{-1})$ speeds of ponies $(110–170 \, kg)^{26}$, and even the preferred trotting speed predicted for a 500-kg quadruped[25].

Most cursorial quadrupeds such as zebra, antelopes, and African hunting dogs trot when running long distances[14], but a few such as hyenas and wildebeest are known to run long distances using a low-speed gallop (typically a canter)[13]. When galloping, species with high sustainable speeds such as dogs or horses can usually outrun humans. The maximum sustainable ($\sim$10–15 min) galloping speed predicted for a 65-kg quadruped is $7.7 \, m \, s^{-1}$, and elite racing horses can gallop 10 km at $8.9 \, m \, s^{-1}$ (refs 25, 27). However, human ER speeds are quite comparable to the preferred galloping speeds that cursors use over longer distances and times. Minetti[27] has shown that sustainable galloping speeds in horses decline considerably for runs longer than 10–15 min, accounting for the average daytime speed of $5.8 \, m \, s^{-1}$ at which long-distance postal horses were consistently run for millennia. Wildebeests ($\sim$100 kg) prefer to canter at $5.1 \, m \, s^{-1}$ (ref. 13). Well-conditioned human runners exceed the predicted preferred galloping speed for a 65-kg quadruped[25] and can occasionally outrun horses over the extremely long distances that constrain these animals to optimal galloping speeds, typically a canter (Fig. 2a)[9,10].

Humans also perform well at ER by another criterion, sustainable distance. Approximately 10% of Americans habitually jog or run several kilometres a day (the percentage is higher if one includes treadmill exercise and related sports)[28]. Fit human amateurs can regularly run 10 km, and longer distances such as marathons (42.2 km) are achieved by tens of thousands of people each year. Such distances are unknown if not impossible for any other primate, but are comparable to those observed in specialized mammalian cursors in open habitats. African hunting dogs travel an average of 10 km per day, and wolves and hyenas travel on average 14 and $19 \, km \, day^{-1}$, respectively[14]. This is not to say that humans can outdistance specialized quadrupeds. Some horse and dog breeds, for example, can be made to run more than $100 \, km \, day^{-1}$ while carrying or pulling a human. Such extreme and human-induced feats, however, should not detract from the fact that humans can and do run long distances well, despite a primate ancestry.

The one category in which humans perform poorly compared to many quadrupeds is the energetic cost of running. The mass-adjusted COT of human running is about 50% higher than a typical mammal, including other primates[12]. Compared to the only value measured for a chimpanzee (a 17.5-kg juvenile), human running is 25% less costly in absolute terms, but about 10% more costly when adjusted for body mass[29]. Interestingly, other endurance cursors such as wolves and African hunting dogs also have high mass-adjusted COT relative to the average mammal[12]. One important characteristic of human ER may be its range of accessible economical speeds. Horses have U-shaped COT curves with narrow ranges of preferred speeds for trotting and galloping and gait transitions that minimize cost, thereby achieving an effectively flat COT curve that excludes many speeds within the aerobic range (Fig. 2b)[26]. It is not known whether other quadrupedal cursors such as dogs have U-shaped COT curves, but human runners differ from horses in employing a single gait, with a flat COT curve at all but the fastest endurance speeds[9,16]. Like another group of cursorial bipeds, kangaroos and wallabies, humans are thus able to adjust running speed continuously without change of gait or metabolic penalty over a wide range of speeds. Further research is necessary to determine whether other cursors are capable of such a broad range of economic speeds.

Structural bases and fossil evidence for endurance running

The human capacity for ER raises several questions. What features make ER possible? When do these features first appear in the fossil record? How might such features relate to adaptations for bipedal walking? Many of the anatomical and physiological features involved in running are well studied in mammals, including humans, but most have not been explicitly evaluated in the human fossil record. A useful approach is to consider separately the evidence for structural features relevant to four types of demands posed by ER: energetics, strength, stabilization and thermoregulation. The skeletal traces of these features, and the
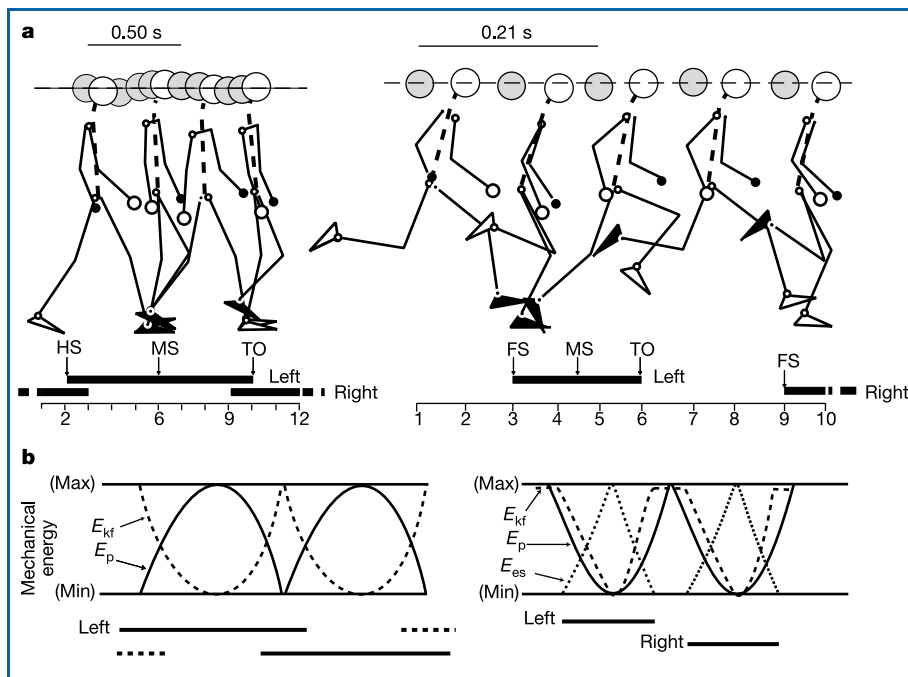

Figure 1 Comparisons of walking and running.
a, Kinematics of walking (left) and running (right), from plates 4 and 18 of ref. 64. During walking, the head and centre of gravity are lowest near toe-off (TO) and highest at mid-stance (MS) where the leg is relatively straight. During running, the head and centre of gravity are highest during the aerial phase and lowest at MS, when the hip, knee and ankle are flexed; the trunk is also more inclined and the elbow more flexed.
b, Biomechanical contrasts between human gaits. During walking, an inverted pendulum mechanism exchanges forward kinetic energy (E_{kf}) for gravitational potential energy (E_p) between heelstrike (HS) and MS; the exchange is reversed between MS and TO. During running, a mass-spring mechanism causes E_p and E_{kf} to be in phase, with both energies declining rapidly to minima between footstrike (FS) and MS. Leg tendons and ligaments partially convert decreases in E_p and E_{kf} to elastic strain energy (E_{es}) during the first half of the stance, which is subsequently released through recoil between MS and TO.

evidence for their first presence in the fossil record, are summarized in Table 1 and illustrated in Fig. 3. Several issues need to be kept in mind when evaluating these features.

First, it is useful to distinguish between structures that benefit both walking and running from those that are specific to the unique biomechanics of running and are functionally unrelated to walking. Second, the limitations of the fossil record complicate our ability to test evolutionary hypotheses concerning many structural modifications that are derived in humans relative to chimpanzees. Some, such as Achilles tendon length, leave no clear skeletal evidence—rendering uncertain their first appearance. Others, particularly in the foot, are not yet adequately sampled in the fossil record to make it possible to identify their origins.

Energetics

Humans exhibit many musculoskeletal specializations for bipedalism. Given the fundamental biomechanical contrasts between walking and running, which features are specifically relevant to the energetic cost of running? As noted above, the mass-spring mechanics of running differ from the pendular mechanics of walking: running uses a compliant limb in which muscles and tendons in the legs sequentially store and then release strain energy during the stance phase of the stride cycle. In contrast to apes, human legs have many long spring-like tendons connected to short muscle fascicles that can generate force economically[30]. These springs (see Fig. 3) can have comparatively little effect on energy savings during an inverted pendulum-like walk, particularly at heel strike when the limb is not compliant, but are estimated to save approximately 50% of the metabolic cost of running[17,19]. The most important of these springs is the Achilles tendon, which connects the heel with the major plantar flexors of the foot; other elongated tendons that are derived features of the human leg include the iliotibial tract and m. (muscle) peroneus longus[31]. Unfortunately, there are no preserved early *Homo* calcanei, and leg tendon length probably cannot be estimated reliably from attachment sites.

However, the transverse groove into which the Achilles tendon inserts on the posterior surface of the calcaneus is chimpanzee-like in size in three early australopithecine Hadar specimens (AL 333-8, 333-37 and 333-55)[32,33], and contrasts with the substantially wider and taller attachment area characteristic of *H. sapiens*. We hypothesize that, as in modern apes, a developed Achilles tendon was absent in *Australopithecus* and originated at some point after 3 Myr ago, probably in the genus *Homo*.

Another well-developed set of springs important to human running is the longitudinal arch of the foot. During walking, the plantar arch helps to maintain mid-tarsal rigidity for powered plantar flexion during toe-off, and absorbs some impact force (but only after heel strike); during running, the elastic structures of the plantar arch function as a spring, returning approximately 17% of the energy generated during each stance phase[19]. Several features in australopithecine foot bones from Hadar and Sterkfontein (STW 573) suggest that some sort of plantar arch was present, including an elongated lateral cuneiform and insertions for the plantar ligaments[4,34,35]. But analyses of the Hadar and Sterkfontein specimens suggest that they may have had a partial arch only, as indicated by the enlarged medial tuberosity of the navicular, which is also enlarged and weight-bearing in chimpanzees, but is diminutive and not weight-bearing in *Homo*[36]. In addition, for the plantar arch to be an effective spring during running, the transverse tarsal joint must restrict rotation between the hind foot and the anterior tarsals, allowing passive stretching of the plantar ligaments during a mid-foot strike. In humans, this rotation is restricted primarily by a projecting medial flange on the proximal cuboid, which causes the calcaneocuboid joint to form a close-packed position following several degrees of rotation[37]. There are no preserved early *H. erectus* feet, but this feature—together with a fully adducted big toe—is first apparent in the OH 8 foot[4,36,37], which is generally ascribed to *H. habilis*.

An additional energetic factor to consider is stride length. Unlike most quadrupeds[25], humans increase speed during ER mostly by
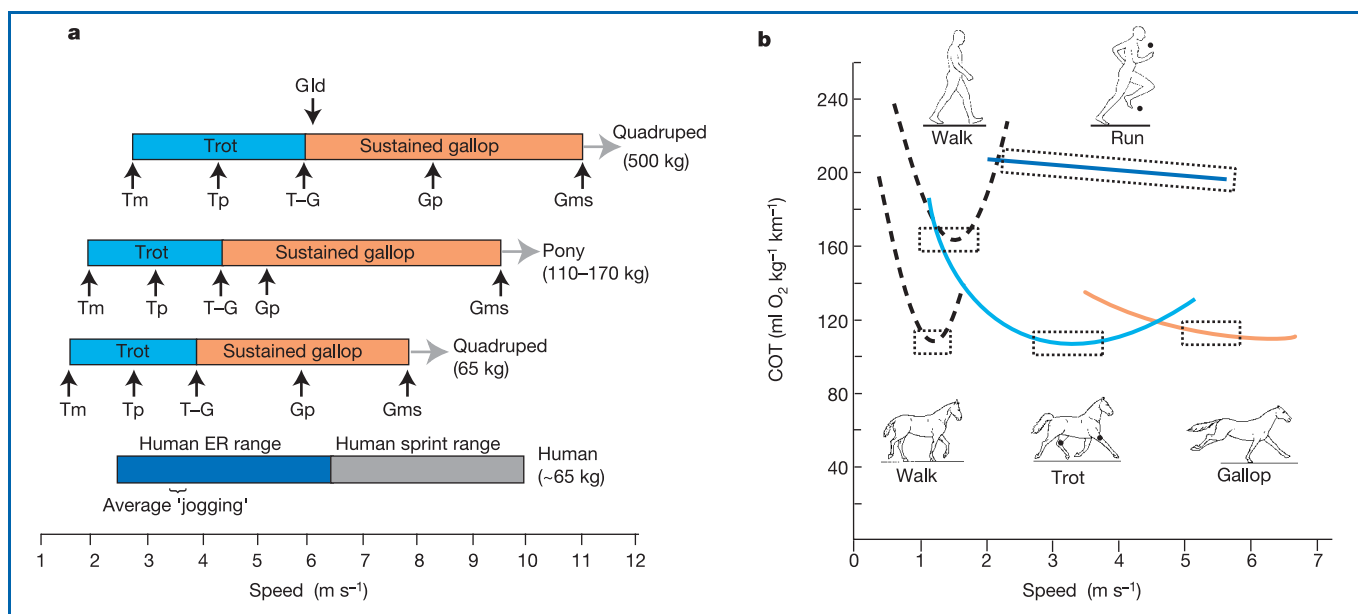

Figure 2 Comparative ER performance in humans and quadrupeds. **a**, Range of speeds for human ER and sprinting, and minimum trot (Tm), preferred trot (Tp), trot–gallop transition (T–G), preferred gallop (Gp), and maximum sustained gallop (Gms) for ponies (ref. 26), and predicted for quadrupeds of 65 and 500 kg (ref. 25). Also indicated is Gld, the optimal long distance (~20 km), daytime galloping speed for horses (ref. 27). Note that quadrupeds sprint at speeds above Gms. **b**, Comparison of the metabolic cost of transport (COT) in humans and ponies[9,16,17]. Both species have U-shaped COT curves for walking, and trotting has a similar-shaped curve in the horse, but the human COT is essentially flat at ER speeds. Preferred speeds (dotted rectangles) correspond to the most energy-efficient speeds in horses and walking humans, but speed selection is unrestricted in human ER. Note also that human running, like quadrupedal trotting, involves synchronized movements of diagonally opposite appendages (dots).

increasing stride length rather than rate (Fig. 4). Stride lengths in humans during ER are typically more than 2 m, and can exceed 3.5 m in elite runners[21], approximately a metre longer than the strides predicted for a 65-kg quadruped[25] or measured in chimpanzees[38] at the same speeds, even when galloping (Fig. 4a). Long absolute (rather than relative) stride lengths in humans are made possible by a combination of effective leg springs (see above) and relatively long legs. Long legs benefit walking by increasing optimum walking speed, but they also increase ground contact time in both walking and running[15]. Relatively long contact times may be advantageous for ER because the inverse of contact time has been found to correlate across species with the energetic cost of running (running is priced by the step)[39]. Long legs relative to body mass, typical of most specialized cursors, first appear unequivocally in hominids 1.8 Myr ago with *H. erectus*, whose relative leg length (assessed from the femur) is possibly up to 50% greater than in *Australopithecus afarensis*[4]. Leg length in *H. habilis* (estimated from the OH 62 skeleton) and other specimens as early as 2.5 Myr ago is currently the subject of debate[40].

Oscillating long legs, however, increases the energy cost of running in proportion to the limb's mass moment of inertia. Reductions in distal limb mass have little effect on the energetics of walking but produce substantial metabolic savings during ER, roughly proportional to the square of the distance of the mass from the hip. Redistributing 3.6 kg from the ankles to the hip, for example, decreases the metabolic cost of human running at slow speeds ($2.6\,\mathrm{m\,s^{-1}}$) by 15% (ref. 41). Although we do not know the relative mass of the distal limb in fossil hominids, humans differ from australopithecines[4,32], and resemble many specialized cursors in having more compact feet and relatively short toes; the human foot is only 9% of total leg mass, compared to 14% in chimpanzees[42]. Humans also have relatively low stride rates at ER speeds, even lower than are predicted for a 500-kg quadruped[25] (Fig. 4b). Low stride rates that increase little in the ER range reduce the force required to oscillate the heavy legs (30% of body mass in humans, compared to 18% in chimpanzees[42]) and may favour greater

reliance on more slowly contracting, oxidative and fatigue-resistant muscle fibres, which are relatively more abundant in the legs of competitive distance runners than in sprinters[43]. The high percentage of slow-twitch muscle fibres necessary for endurance running may have originated in humans from a novel null mutation of the *ACTN3* gene[44].

Skeletal strength

Another factor to consider when evaluating the evolution of ER in humans is skeletal strength. Running exposes the skeletal system to much higher stresses than walking, especially when the foot collides with the ground, producing a shock wave that passes up the body from the heel through the spine to the head. Peak vertical ground reaction forces (GRFs) at heel strike are approximately twice as high during running than during walking and may approach 3–4 times body weight at higher ER speeds[45]. Human runners reduce these stresses to some extent through limb compliance and mid-foot striking (thereby also storing elastic strain energy in the leg and foot), but must otherwise dissipate impact forces within their bones and joints. One strategy to lower joint stress is to expand joint surfaces, spreading forces over larger areas. Many studies have found that compared to both *Pan* and *Australopithecus*, *Homo* has substantially larger articular surface areas relative to body mass in most joints of the lower body, including the femoral head and knee[6,7], the sacroiliac joint[46,47], and the lumbar centra[47]. Enlargement of these joints, which is not matched in the upper limb of *Homo*[6], lowers the stresses that impact forces generate at heel strike during walking, but would contribute more critically to dissipate the much higher impact loads generated in running. Another possible modification of the pelvis for resisting the stresses associated with running is enlargement of the iliac pillar in early *H. erectus*[4,46]. Humans may also have a larger cross-sectional area of the calcaneal tuber relative to body mass than australopithecines[33].

Both walking and running also cause diaphyseal loading, which is higher in running and increases relative to body mass as a function

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Table 1 **Derived features of the human skeleton with cursorial functions**

Feature	Functional role	W/R*	Earliest evidence
Enlarged posterior and anterior semicircular canals	Head/body stabilization	R	*H. erectus*
Expanded venous circulation of neurocranium	Thermoregulation	R > W	*H. erectus*
More balanced head	Head stabilization	R	*H. habilis*
Nuchal ligament (1)	Head stabilization	R	*H. habilis*
Short snout (2)	Head stabilization	R > W	*H. habilis*
Tall, narrow body form	Thermoregulation	R > W	*H. erectus*
Decoupled head and pectoral girdle (3)	Counter-rotation of trunk versus head	R	*H. erectus?*
Low, wide shoulders (4)	Counter-rotation of trunk versus hips	R	*H. erectus?*
Forearm shortening (5)	Counter-rotation of trunk		*H. erectus?*
Narrow thorax (6)	Counter-rotation of trunk versus hips	R	*H. erectus?*
Narrow and tall waist between iliac crest and ribcage (7)	Counter-rotation of trunk versus hips	R	*H. erectus?*
Narrow pelvis (8)	Counter-rotation of trunk versus hips	R	*Homo?*
	Stress reduction	R > W	
Expanded lumbar centra surface area (9)	Stress reduction	R > W	*H. erectus*
Enlarged iliac pillar (10)	Stress reduction	R > W	*H. erectus*
Stabilized sacroiliac joint	Trunk stabilization	R	*H. erectus*
Expanded surface area for mm. erector spinae origin (11)	Trunk stabilization	R	*H. erectus*
Expanded surface area for m. gluteus maximus origin (12)	Trunk stabilization	R	*H. erectus*
Long legs (13)	Stride length	R,W	*H. erectus*
Expanded hindlimb joint surface area (14)	Stress reduction	R > W	*H. erectus*
Shorter femoral neck (15)	Stress reduction	R > W	*H. sapiens*
Long Achilles tendon (16)	Energy storage	R	*Homo?*
	Shock absorbtion	R	
Plantar arch (passively stabilized) (17)	Energy storage	R	*Homo?*
	Shock absorbtion	R > W	
	Powered plantarflexion	R > W	
Enlarged tuber calcaneus (18)	Stress reduction	R > W	*Homo?*
Close-packed calcaneocuboid joint	Energy storage	R	*H. habilis* (OH 8)
	Stability during plantarflexion	R > W	
Permanently adducted hallux (19)	Stability during plantarflexion	R > W	*H. habilis* (OH 8)
Short toes (20)	Stability during plantarflexion	R > W	*H. habilis* (OH 8)
	Distal mass reduction	R > W	

*W,R indicate traits that enhance performance in endurance walking and endurance running, respectively; R > W indicates traits that benefit both walking and ER, but which have a greater effect on ER. Numbers in parentheses correspond to those in Fig. 3a and c.

of speed[48]. Like *Pan* and early *Homo*, australopithecines have robust femoral shafts relative to body mass, but they are less wide transversely than in early *Homo*[7]. Although the distinctly shorter femoral neck of humans compared to *Pan* or *Australopithecus* decreases the mechanical advantage of the hip abductors, it might also facilitate running by reducing bending moments in the femoral neck. The reduction in interacetabular hip breadth in *Homo* also reduces lateral bending moments on the pelvis and lower back generated at footstrike, and likewise helps minimize the angular momentum in the trunk caused by rapid oscillation of long, heavy legs[49].

Stabilization

Bipedal gaits are inherently unsteady, but several differences between running and walking call for special mechanisms during running to help ensure stabilization and balance. Most obviously, the trunk and neck of human runners are more forwardly inclined during running than walking (Fig. 1a), resulting in a greater tendency to pitch forward, especially at heel strike. *Homo* has a number of derived features that enhance trunk stabilization, including expanded areas on the sacrum and the posterior iliac spine for the attachment of the large erector spinae muscles, and a greatly enlarged m. gluteus maximus[4,46]. The latter muscle, whose increased size is among the most distinctive of all human features, is strongly recruited in running at all speeds but not in walking on level surfaces[50]. In addition, the transverse processes of the sacrum are also relatively larger in *Homo* than *Australopithecus*, suggesting a more mechanically stable sacroiliac joint[34].

Independent rotations within the trunk play a crucial role in dynamic stabilization during human running and may help to
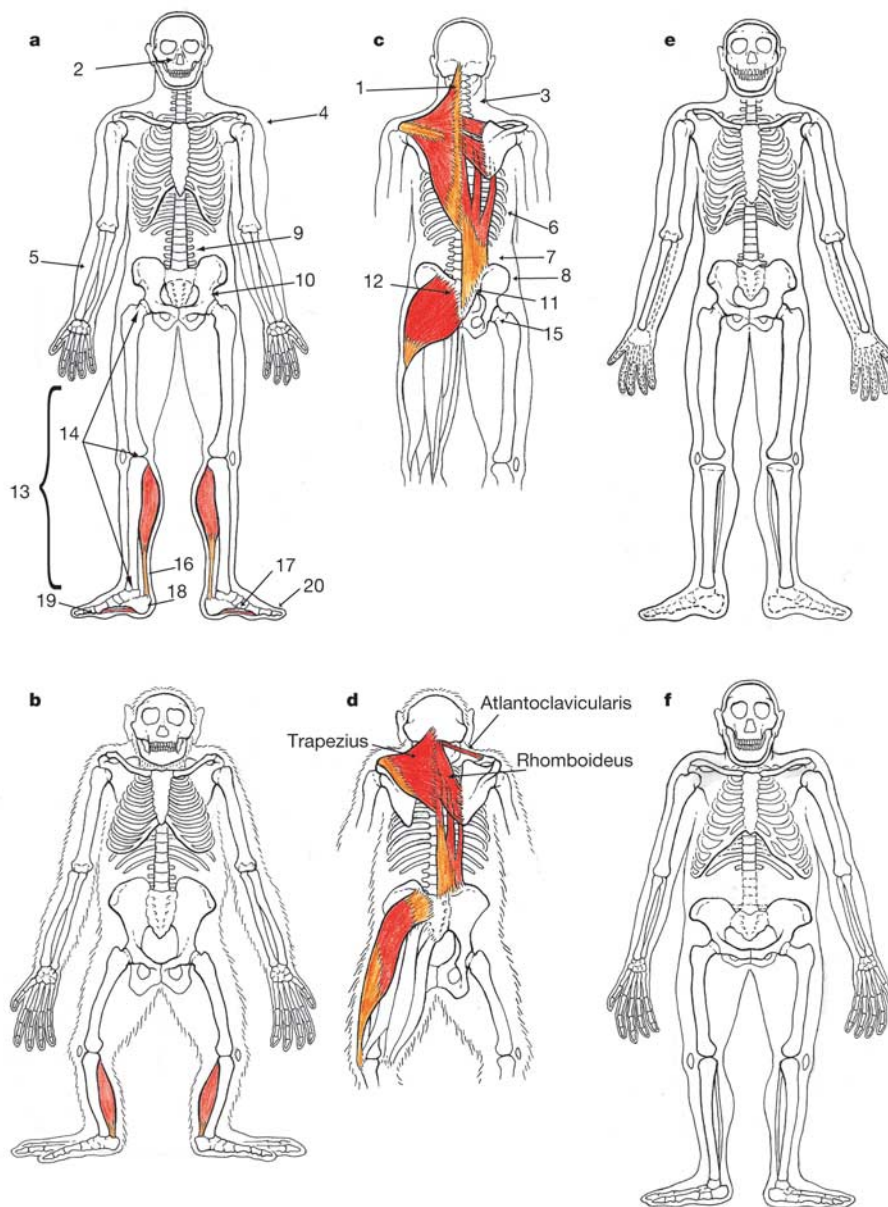

Figure 3 Anatomical comparisons of human, chimpanzee, *H. erectus* and *A. afarensis*. **a**, **c**, Anterior and posterior views of human, enumerating features related to endurance running listed in Table 1. **b**, **d**, Anterior and posterior views of chimpanzee. Labelled muscles connect the head and neck to the pectoral girdle and are reduced or absent in humans. **e**, Reconstruction of *H. erectus* based primarily on KNM-WT 15000 (from refs 4, 65); **f**, reconstruction of *A. afarensis* based primarily on AL-288 (from refs 4, 66).

explain several derived features of *Homo*. In a walk, one leg is always on the ground, enabling the abductors and medial rotators of the stance hip to counteract the inertially induced rotation of the trunk (about its vertical axis) generated by the forward acceleration of the swing leg. However, during the aerial phase of running, leg acceleration generates even larger torques that cannot be counteracted by ground forces. These potentially destabilizing forces are offset by the opposing torques produced by counter-rotation of thorax and arms (but not the head)[49]. At least three derived structural modifications in the hips and shoulder permit humans to generate these counter-balancing torques. First, humans are capable of a substantially greater degree of isolated rotation of the trunk relative to the hips compared to apes[4], thanks to an elongate, narrow waist that vertically separates the lower margin of the thorax from the pelvis. This configuration is fully developed in *H. erectus*[51]. *Australopithecus* may have had a tall waist, but its broad, chimpanzee-shaped thorax and broad pelvis (possibly related to gut size[52]) suggest a relatively wider waist than in *Homo*. Second, *Homo* differs from *Pan* and possibly from *Australopithecus* in having greater structural independence of the pectoral girdle and head. Chimpanzees have an inverted funnel-shaped upper thorax, with narrow and habitually elevated ('shrugged') shoulders, and extensive muscular connections (mm. (muscles) rhomboideus, atlantoclavicularis, trapezius superior) between the shoulder and the head–neck complex that are either absent or much reduced in *Homo*[4,31]. The cleidocranial portion of the m. trapezius is the sole muscular connection in humans between the pectoral girdle and head (Fig. 3c, d). Cranially oriented glenoid cavities (present in *Australopithecus*),

elevated shoulders and strong muscular connections to the head and neck are functionally advantageous for climbing[34], pose no obvious hindrance to bipedal walking, but would tend to impede the independent counter-rotations of the pectoral girdle and arms necessary to counter-balance the legs in running, and to minimize axial rotation of the head. (Decoupling of the head and pectoral girdle may also be advantageous for throwing.) Finally, the wide shoulders characteristic of *Homo* act to increase the counterbalancing moments generated by arm-swinging, while also permitting energy-saving reductions in forearm mass. Reductions in the forearm of *Homo* (50% less massive relative to total body mass in humans than chimpanzees[4,42]), substantially lower the muscular effort required to maintain the stereotypically flexed elbow during ER.

Running also poses problems for head stabilization. Unlike quadrupeds, humans have vertically oriented necks that are less able to counteract the greater tendency of the head to pitch forward at foot strike during running than walking. Such inertial accelerations would be reduced in *Homo* relative to *Australopithecus* and *Pan* by a combination of decreased facial length and occipital projection behind the foramen magnum[4]. In addition, the radius of the posterior semicircular canal is significantly larger in *Homo* than in *Pan* or *Australopithecus*[53], presumably increasing the sensitivity of sensory perception to head pitching in the sagittal plane, which is potentially much greater during running than walking. Another possible structural modification relevant to running is the nuchal ligament, a convergent feature in *Homo* (first evident in KNM-ER 1813) and other mammals that are either cursorial (for example, dogs, horses, hares) or have massive heads (elephants)[54]. Interestingly, a nuchal ligament is absent in chimpanzees[4,31] and apparently in australopithecines (as evinced by the absence of a median nuchal line).

Thermoregulation and respiration

A final physiological challenge to consider is heat. Adaptations to maintain stable body temperature have long been considered important for long-distance walking in open, hot environments. However, running generates so much endogenous heat that sustained running is considerably more limited by thermoregulatory capabilities than is walking. As noted by refs 9 and 55, humans possess many derived features related to heat dissipation, including elaboration and multiplication of eccrine sweat glands for evapotranspiration, and reduced body hair (which increases convection rates). We do not know when these non-musculoskeletal traits evolved, but several other derived features of *Homo* are possible mechanisms for dissipating metabolic heat, and could have been especially important for ER in hot environments. These include a narrow, elongated body form[56], and possibly an elaborated cranial venous circulation (for example, more accessory foramina in the cranial vault, and diploic expansion[57]). The latter may use venous blood that has been cooled by sweating in the face and scalp to cool, via countercurrent heat exchange in the cavernous sinus, hot arterial blood in the internal carotid artery before it reaches the brain[58]. Another derived feature of humans is the tendency for mouth breathing (but not panting) during strenuous activity. Nasal breathing, typical of apes, offers too much resistance within the relatively small human nasopharynx to support the high ventilatory demands of strenuous activities such as ER[59]. Human distance runners are thus obligate mouth breathers, permitting higher airflow rates with less resistance and muscular effort; mouth breathing is also a more effective means of unloading excess heat during expiration.

Evolutionary hypotheses

Many hypotheses have been proposed for the role of walking (particularly long-distance trekking) in human evolution. Given human ER performance capabilities, as well as the many derived features that appear to make them possible, it is also necessary to ask
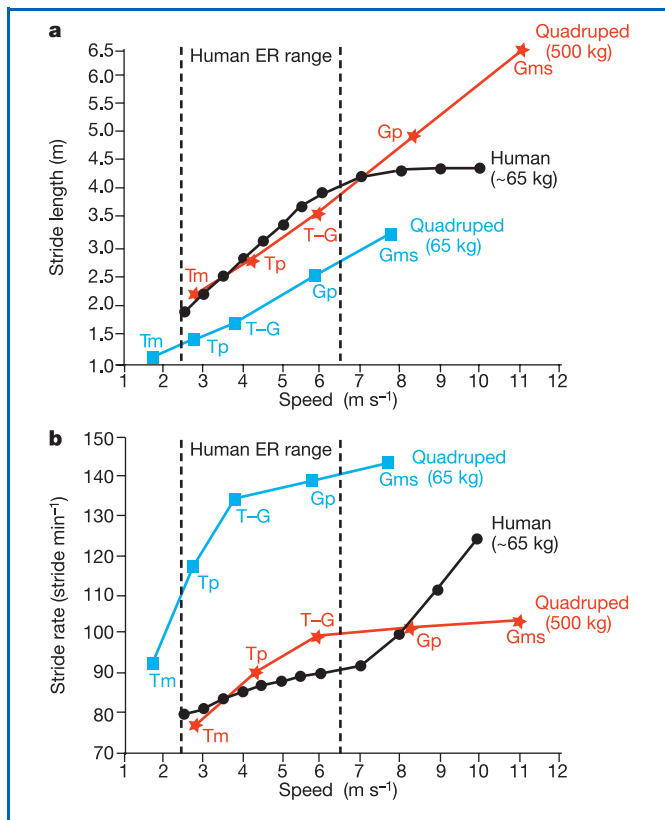

Figure 4 Comparison of stride length (**a**) and stride rate (**b**) contributions to running speed in humans[21,64], and in quadrupedal mammals (calculated from ref. 25) for various gaits (as in Fig. 2a). A stride is a complete locomotor cycle (two steps for a human). Compared to similar-sized quadrupeds, humans have relatively long stride lengths and relatively low stride rates in the ER range. Humans increase speed within the ER range primarily by increasing stride length not rate.

whether, when and why long-distance running may have played a role in human evolution. Although the fossil record is inadequate to pinpoint the origin of all the morphological features that contribute to human ER performance capabilities, most of the major structural bases of ER that can be observed in the skeleton are present in early *H. erectus* (Table 1). Despite disagreement over the hypodigm and systematic position of *H. habilis*[8], several specimens that are generally attributed to this species (for example, the OH 8 foot and the KMN-ER 1813 cranium), also have a few derived features consistent with cursorial function (Table 1). It is thus reasonable to conclude that ER capabilities in human evolution originated in the genus *Homo*. Further data, however, are needed to test this hypothesis more fully. We currently lack any *H. erectus* feet, few postcranial remains are attributed to *H. habilis* or *H. rudolfensis*, and some key adaptations such as the length of the Achilles tendon are difficult and perhaps impossible to assess from fossils. Although the postcranial remains of australopithecines indicate that they walked habitually, their lack of any features associated with ER suggests that, like chimps[30], they probably did not run long distances well or frequently in the less-open habitats in which they lived.

The ER capabilities of *Homo* raise several additional questions, the first being whether long-distance running was an important behaviour in human evolution or merely the by-product of enhanced walking capabilities. Traditional arguments have favoured the latter hypothesis; several of the derived features of *Homo* in Table 1 are proposed as adaptations to improve long-distance walking performance in more arid, open habitats (for example, refs 5–8). These features include relatively longer legs, larger hindlimb and vertebral joint surfaces, narrower waists and shorter toes. Yet walking alone cannot account for many of the other derived features in Table 1 because the mass-spring mechanics of running, which differ fundamentally from the pendular mechanics of walking, require structural specializations for energy storage and stabilization that have little role in walking. Such specialized structures include: an extensive system of springs in the leg and foot that effectively store and release significant elastic energy during running; hypertrophied gluteus maximus and spinal extensor muscles that contract strongly to stabilize the trunk in running but not walking; and an elongate, narrow waist in combination with a low, wide, decoupled shoulder girdle that have an essential stabilizing function only in running.

Two additional lines of evidence suggest that ER capabilities in *Homo* are not solely by-products of selection for long-distance walking. First, sustained running poses extreme mechanical and thermoregulatory challenges beyond those encountered in distance walking. Expanded joint surfaces in the spine, hip, and legs, along with multiple specializations for shedding excess body heat (for example, sweating, hairlessness, cranial cooling systems), would be useful for prolonged walking in hot environments, but they would have been essential to tolerate the considerably higher impulsive loads and endogenous heat produced by distance running. Second, a few derived features of *Homo* that improve ER capabilities (notably forearm shortening and decoupling of the head and pectoral girdle) are unrelated to walking, but would have hindered arboreal locomotor capabilities. Thus some of the differences between *Homo* and *Australopithecus* that have been attributed to selection for more efficient long-distance walking may instead have evolved for ER, thereby helping to make *Homo* the first fully terrestrial hominoid.

Considering all the evidence together, it is reasonable to hypothesize that *Homo* evolved to travel long distances by both walking and running. New fossils and more detailed analyses of the existing fossil record are needed to test whether these two locomotor capabilities emerged concurrently or whether ER evolved after selection for long-distance walking. An even more difficult task is to determine what behaviours selected for ER in the first place. Why would early *Homo* run long distances when walking is easier, safer and less costly? One possibility is that ER played a role in helping hominids exploit protein-rich resources such as meat, marrow and brain first evident in the archaeological record at approximately 2.6 Myr ago[60], coincident with the first appearance of *Homo*. Testing whether ER was employed in hunting or scavenging will be challenging given the limitations of the archaeological and ethnographic records. ER is not common among modern hunter-gatherers, who employ many technologies to hunt (for example, bows and arrows, nets and spear-throwers), thereby minimizing the need to run long distances. But Carrier[9] has hypothesized that ER evolved in early hominids for predator pursuit before these inventions in the Upper Palaeolithic (about 40,000 yr ago). ER may have helped hunters get close enough to throw projectiles, or perhaps even to run some mammals to exhaustion in the heat. Although such demanding strategies have been occasionally documented among modern foragers (see ref. 61), they might have been too energetically expensive and low-yield for the benefits to have outweighed the costs.

Another hypothesis to explore is that ER was initially useful for effective scavenging in the open, semi-arid environments apparently inhabited by early *Homo*. If early hominids were regularly scavenging marrow, brain and other tissues from carcasses, then ER would have helped hominids to compete more effectively for these scattered and ephemeral resources. Wild dogs and hyenas often rely upon remote olfactory or visual cues such as circling vultures to identify scavenging opportunities, and then run long distances to secure them[13,14]. Early *Homo* may thus have needed to run long distances to compete with other scavengers, including other hominids. This hypothesis is difficult to test because modern hunter-gatherers tend to scavenge only opportunistically. However, similar strategies of 'pirating' meat from carnivores are sometimes practised by the Hadza in East Africa[62] and perhaps were more common in open habitats before the invention of technologies such as the bow and arrow.

Additional research will help to clarify and test when and how ER capabilities evolved in humans, and to examine more thoroughly their implications for human evolution. For example, it is known that major increases in encephalization occurred only after the appearance of early *Homo*[4,8]. The hypothesis that ER evolved in *Homo* for scavenging or even hunting therefore suggests that ER may have made possible a diet rich in fats and proteins thought to account for the unique human combination of large bodies, small guts, big brains and small teeth[52,63]. Today, ER is primarily a form of exercise and recreation, but its roots may be as ancient as the origin of the human genus, and its demands a major contributing factor to the human body form. □

1. Haile-Selassie, Y. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* **412**, 178–181 (2001).
2. Galik, Y. *et al.* External and internal morphology of the BAR 1002′00 *Orrorin tugenensis* femur. *Science* **305**, 1450–1453 (2004).
3. Ward, C. V. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *Yb. Physical Anthropol.* **35**, 185–215 (2002).
4. Aiello, L. & Dean, M. C. *An Introduction to Human Evolutionary Anatomy* (Academic, London, 1990).
5. Rose, M. D. in *Origine(s) de la Bipédie chez les Hominides* (eds Coppens, Y. & Senut, B.) 37–49 (CNRS, Paris, 1991).
6. Jungers, W. L. Relative joint size and hominid locomotor adaptations with implications for the evolution of hominid bipedalism. *J. Hum. Evol.* **17**, 247–265 (1988).
7. Ruff, C. B. *et al.* in *Primate Locomotion: Recent Advances* (ed. Strasser, E.) 449–469 (Plenum, New York, 1998).
8. Wood, B. & Collard, M. The human genus. *Science* **284**, 65–71 (1999).
9. Carrier, D. R. The energetic paradox of human running and hominid evolution. *Curr. Anthropol.* **25**, 483–495 (1984).
10. Heinrich, B. *Why We Run: A Natural History* (Harper Collins, New York, 2002).
11. Garland, T. Jr. The relation between maximal running speed and body-mass in terrestrial mammals. *J. Zool.* **199**, 157–170 (1983).
12. Taylor, C. R., Heglund, N. C. & Maloiy, G. M. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1–21 (1982).
13. Pennycuick, C. J. in *Serengeti: Dynamics of an Ecosystem* (eds Sinclair, A. R. E. & Norton-Griffiths, M.) 164–184 (Univ. Chicago Press, Chicago, 1979).

14. Holekamp, K. E., Boydston, E. E. & Smale, E. in *How and Why Animals Travel in Groups* (eds Boinski, S. & Garber, P.) 587–627 (Univ. Chicago Press, Chicago, 2000).

15. Alexander, R. M. Optimum walking techniques for quadrupeds and bipeds. *J. Zool. Lond.* **192**, 97–117 (1980).

16. Margaria, R., Cerretelli, P., Aghemo, P. & Sassi, G. Energy cost of running. *J. Appl. Physiol.* **18**, 367–370 (1963).

17. Alexander, R. M. Energy-saving mechanisms in walking and running. *J. Exp. Biol.* **160**, 55–69 (1991).

18. Cavagna, G. A., Thys, H. & Zamboni, A. The sources of external work in level walking and running. *J. Physiol. Lond.* **262**, 639–657 (1976).

19. Ker, R. F. *et al.* The spring in the arch of the human foot. *Nature* **325**, 147–149 (1987).

20. Farley, C. T., Glasheen, J. & McMahon, T. A. Running and springs: speed and animal size. *J. Exp. Biol.* **185**, 71–86 (1993).

21. Cavanagh, P. R. & Kram, R. Stride length in distance running: velocity, body dimensions, and added mass effects. *Med. Sci. Sports Exerc.* **21**, 467–479 (1989).

22. Hunt, K. D. Mechanical implications of chimpanzee positional behavior. *Am. J. Phys. Anthropol.* **86**, 521–536 (1991).

23. Isbell, L. A. *et al.* Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo. Am. J. Phys. Anthropol.* **105**, 199–207 (1998).

24. Alexander, R. M., Jayes, A. S. & Ker, R. F. Estimates of energy cost for quadrupedal running gaits. *J. Zool. Lond.* **190**, 155–192 (1980).

25. Heglund, N. C. & Taylor, C. R. Speed, stride frequency and energy cost per stride. How do they change with body size and gait? *J. Exp. Biol.* **138**, 301–318 (1988).

26. Hoyt, D. F. & Taylor, C. R. Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240 (1981).

27. Minetti, A. E. Physiology: efficiency of equine express postal systems. *Nature* **426**, 785–786 (2003).

28. National Center for Chronic Disease Prevention and Health Promotion. *Participation in Physical Activities: Adults Aged 18 and Over* (National Health Information Survey, 1998, now age-adjusted to 2000 population); (http://www.cdc.gov/nccdphp/dnpa/physical/stats/pasports.htm).

29. Taylor, C. R. & Rowntree, V. J. Running on two or on four legs: which consumes more energy? *Science* **179**, 186–187 (1973).

30. Thorpe, S. K. *et al.* Dimensions and moment arms of the hind- and forelimb muscles of common chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* **110**, 179–199 (1999).

31. Swindler, D. R. & Wood, C. D. *An Atlas of Primate Gross Anatomy: Baboon, Chimpanzee and Man* (Univ. Washington Press, Seattle, 1973).

32. Susman, R. L., Stern, J. T. & Jungers, W. L. Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* **43**, 113–156 (1984).

33. Latimer, B. & Lovejoy, C. O. The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *Am. J. Phys. Anthropol.* **78**, 369–386 (1989).

34. Stern, J. T. & Susman, R. L. The locomotor anatomy of *Australopithecus afarensis. Am. J. Phys. Anthropol.* **60**, 279–317 (1983).

35. Clarke, R. J. & Tobias, P. V. Sterkfontein Member 2 foot bones of the oldest South African hominid. *Science* **269**, 521–524 (1995).

36. Harcourt-Smith, W. E. H. *Form and Function in the Hominoid Tarsal Skeleton* Thesis, Univ. College London (2002).

37. Lewis, O. J. *Functional Morphology of the Evolving Hand and Foot* (Oxford Univ. Press, Oxford, 1989).

38. Reynolds, T. R. Stride length and its determinants in humans, early hominids, primates, and mammals. *Am. J. Phys. Anthropol.* **72**, 101–115 (1987).

39. Kram, R. & Taylor, C. R. Energetics of running: a new perspective. *Nature* **346**, 265–267 (1990).

40. Haeusler, M. & McHenry, H. M. Body proportions of *Homo habilis* reviewed. *J. Hum. Evol.* **46**, 433–465 (2004).

41. Myers, M. J. & Steudel, K. Effect of limb mass and its distribution on the energetic cost of running. *J. Exp. Biol.* **116**, 363–373 (1985).

42. Zihlman, A. L. & Brunker, L. Hominid bipedalism: then and now. *Yb. Physical Anthropol.* **22**, 132–162 (1979).

43. Mero, A., Jaakkola, L. & Komi, P. V. Relationships between muscle fibre characteristics and physical performance capacity in trained athletic boys. *J. Sports Sci.* **9**, 161–171 (1991).

44. Yang, N. *et al.* ACTN3 genotype is associated with human elite athletic performance. *Am. J. Hum. Genet.* **73**, 627–631 (2003).

45. Keller, T. S. *et al.* Relationship between vertical ground reaction force and speed during walking, slow jogging, and running. *Clin. Biomech.* **11**, 253–259 (1996).

46. Rose, M. D. A hominine hip bone, KNM-ER 3228, from East Lake Turkana, Kenya. *Am. J. Phys. Anthropol.* **63**, 371–378 (1984).

47. Sanders, W. J. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. *J. Hum. Evol.* **34**, 249–302 (1998).

48. Biewener, A. A. & Taylor, C. R. Bone strain: a determinant of gait and speed? *J. Exp. Biol.* **123**, 383–400 (1986).

49. Hinrichs, R. N. in *Biomechanics of Distance Running* (ed. Cavanagh, P. R.) 107–133 (Human Kinetics Books, Champaign, Illinois, 1990).

50. McLay, I. S., Lake, M. J. & Cavanagh, P. R. in *Biomechanics of Distance Running* (ed. Cavanagh, P. R.) 165–186 (Human Kinetics Books, Champaign, Illinois, 1990).

51. Jellema, L. M., Latimer, B. & Walker, A. in *The Nariokotome* Homo erectus *Skeleton* (eds Walker, A. & Leakey, R. E. F.) 294–325 (Harvard Univ. Press, Cambridge, 1993).

52. Aiello, L. & Wheeler, P. The expensive tissue hypothesis: the brain and digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199–221 (1995).

53. Spoor, F., Wood, B. & Zonneveld, F. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature* **369**, 645–648 (1994).

54. Bianchi, M. The thickness, shape and arrangement of the elastic fibres within the nuchal ligament from various animal species. *Anat. Anz. Jena* **169**, 53–66 (1989).

55. Wheeler, P. E. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. *J. Hum. Evol.* **21**, 107–115 (1991).

56. Ruff, C. B. Climate and body shape in hominid evolution. *J. Hum. Evol.* **21**, 81–105 (1990).

57. Falk, D. Brain evolution of *Homo*: the radiator theory. *Behav. Brain Sci.* **13**, 333–381 (1990).

58. Cabanac, M. & Caputa, M. Natural selective cooling of the human brain: evidence of its occurrence and magnitude. *J. Physiol. Lond.* **286**, 255–264 (1979).

59. Niinimaa, V., Cole, P., Mintz, S. & Shephard, R. J. The switching point from nasal to oronasal breathing. *Resp. Physiol.* **42**, 61–71 (1981).

60. Semaw, S. *et al.* 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *J. Hum. Evol.* **45**, 169–177 (2003).

61. Nabokov, P. *Indian Running: Native American History and Tradition* (Ancient City, Santa Fe, New Mexico, 1987).

62. O'Connell, J. F., Hawkes, K. & Blurton-Jones, N. G. Hadza scavenging: implications for Plio-Pleistocene hominid subsistence. *Curr. Anthropol.* **29**, 356–363 (1988).

63. Wrangham, R. W. *et al.* The raw and the stolen: cooking and the ecology of human origins. *Curr. Anthropol.* **5**, 567–594 (1999).

64. Muybridge, E. *The Human Figure in Motion* (Dover, New York, 1985).

65. Walker, A. & Leakey, R. E. F. *The Nariokotome* Homo erectus *skeleton* (Harvard Univ. Press, Cambridge, 1993).

66. Lovejoy, O. Evolution of human walking. *Sci. Am.* **259**, 118–125 (1988).

67. Dillman, C. J. Kinematic analyses of running. *Exercise Sports Sci. Rev.* **3**, 193–218 (1975).

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