The Evolution of the *Homo* Genus as Endurance Running Mammals

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Introduction:

When one thinks of mammals that are good at running, humans are not on the top of the list. Compared to many other mammals, humans are slow and weak. The world's fastest man, Usain Bolt, could easily be beat in a sprint by a squirrel (McDougall, 2011). Humans, however, have a unique ability to run long distances in hot arid climates. This ability is unseen in other primates and unparalleled in other mammals. Humans have many specialized features that allow them to overcome stability, energetic, strength, and thermoregulatory challenges of endurance running (Lieberman and Bramble, 2007). The Endurance Running Hypothesis suggests that endurance running capabilities are a derived trait of *Homo*, that evolved near the origin of the species in response to ecological changes (Liberman, 2009; McDougall, 2011).

Climate changes drove much of human evolution, in that the changing habitats of early hominid species, members of the great ape family, necessitated physical adaptions and adoption of new ecological niches for improved energy acquisition and expenditure (Lieberman, 2016). Fossil evidence, as well as research on the physiological and anatomical bases of endurance running, suggests that many features adapted in early *Homo* for endurance running capabilities (Bramble and Liberman, 2004). *Homo* adapted to become efficient runners which allowed them to fill a new ecological niche of social diurnal carnivores. With endurance abilities, they could outcompete other carnivores before the development of sophisticated weapons via persistence hunting (Bramble and Lieberman 2004, McDougall, 2011). This allowed early *Homo* to obtain meat needed for their expanding brains and give way to a positive energetic feedback cycle crucial to human evolution (Liberman, 2009). It is hypothesized that, under ecological pressures, the *Homo* genus morphologically, physiologically, and behaviorally evolved as endurance running mammals for the sake of more efficient energy acquisition, and such has shaped the bodies, abilities, and health of modern humans.

Early Human Evolution: Climate Change and Energy Acquisition

Homo sapiens evolved in Africa about 315,000 years ago (Dunbar, 2016). We are the only hominins alive today, but fossil evidence reveals that we are related to other members of the human tribe that preceded us for millions of years. Hominins are members of the lineage leading to modern humans after the split from a last common ancestor. Hominids, members of the great ape family, can be traced back to the early Miocene era in Africa about 20 Mya. It is theorized that a common ancestor existed between humans and the great apes that acted as a node of divergence into separate lineages, however, no clear chronological series of species leading to *Homo sapiens* has been identified (Dunbar, 2016). It is likely that *Pan*, chimpanzees, and humans diverged from their last common ancestor about 6-8 Mya. Since the previous node was that of the divergence of *Dryopithecus* into the gorilla lineage and the lineage that became chimpanzees and humans, the last common ancestor of chimps and humans must have been chimpanzee/gorilla-like, forest-dwelling, fruit-eating, knuckle-walkers. The earliest hominins were chimpanzee-like in morphology but had some differences which likely served as adaptations to a more open habitat at the end of the Miocene Epoch. From there the human lineage split into *Australopithecus,* a genus consisting of possibility 8 species of gracile australopithecines, and another lineage that soon after diverged into *Paranthropus,* robust australopithecines, and *Homo*. The radiation of australopithecine involved two separate grades; the gracile australopiths, genus *Australopithecus*, which give rise to the genus *Homo*, and the robust australopiths that survived much longer and cohabitated with early *Homo* (Lieberman, 2009). The human lineage, as currently identified, began with *Australopithecus afarensis*, followed by *Homo habilis, Homo erectus, Homo neanderthalensis*, and, lastly, *Homo sapiens*. There is fossil evidence that suggests some of these species of the *Homo* genus had periods of overlapping coexistence for much of human history (Dunbar, 2016). For this reason, the ancestral history of humans is more accurately described as a "family bush" than a "family tree" (Tuttle, 2018).

The question of why human evolution occurred can be explained by ecological changes necessitating adaptations for improved energy acquisition and expenditure. The human "family bush" began during the Late Miocene Epoch. This time period was characterized by major global climate changes. The climate cooled and dried causing rainforests and evergreens, that were home to many species of apes, to give way to more-open, mosaic habitats of open woodlands, shrublands, and grasslands. A consequence of these changes was that early hominins needed to travel farther to obtain food and there were fewer trees to swing from, causing many species to die out. In surviving hominid species, the diversification of habitats gave rise to behavioral and morphological adaptations in locomotion allowing a shift from arboreal to terrestrial life. It must have been one of the surviving ape lineages from this time that became the common ancestor of the living African great apes and humans (Dunbar, 2016). The adaptation of bipedalism, walking on two legs, allowed hominins to occupy new niches in the continuingly more open habitats that developed (Liberman, 2009). Because of such, obligate terrestrial bipedalism is a defining trait of Hominini (Tuttle, 2016). It is evident that early hominins were bipeds from fossil remains. A significant skeletal indication of bipedalism is ventral positioning of the foramen magnum, the hole in the base of the skull through which the spinal cord passes, so that the neck is pointed straight down when the eyes were pointed forward (Lieberman, 2009). Since animals typically point their eyes in the direction that they are moving, the ventrally located foramen magnum evident in the cranial remains of early hominins indicates that they traveled on two legs with an erect posture. Conversely, the foramen magnum of quadrupedal animals is at the rear of the skull, caudal, so the head and eyes are pointed forward while walking on all fours (Lieberman, 2009). The ventral positioning of the foramen magnum is seen in the earliest reputed fossil hominin, Sahelanthropus tchadensis, which was found in Chad, West Africa and dates to 7 Mya (Dunbar, 2016). Bipedalism would have been a major advantage in a habitat where walking long distances was necessary to get food because bipedal walking is much less costly than knuckle-walking. Studies with modern chimpanzees and humans indicate that chimpanzees spend 75% more energy to move their bodies 1 km by knuckle-walking than humans do by bipedal walking (Lieberman, 2009) Overall, early hominins adapted for less costly locomotion in response to an increasingly open habitat that necessitated traveling greater distances to get food

Another major ecological event marked the origin of the *Homo* genus about 2.5 Mya. During the late Pliocene, the climate continued to cool causing woodlands to shrink and savannahs to expand. In this even more open habitat, nearby food sources were scarce (Tuttle, 2018). Adaptations to this habitat gave rise to both more robust australopiths and the first *Homo*. Robust australopiths had very large and thick teeth, larger muscular faces and jaws, and small bodies and brains. They specialized in eating mechanically demanding, course, and unprocessed food, and were biped walkers, as well as, climbers. *Homo*, on the other hand, adapted for high quality, energy-rich diets. They had larger brains, bigger bodies, smaller teeth, vertical faces, external noses, and were biped walkers and endurance runners. This was the origin of the first hunter-gatherers (Lieberman, 2009). Early *Homo* adapted for the new ecological niche of smart, social, diurnal carnivores and forgers. Unlike earlier hominins who likely maintained plant-based diets, *Homo* ate meat, as evident by their much larger brains and bodies, smaller teeth and jaws, and smaller guts. The only weapon evident at this time, however, was an untipped spear, so early *Homo* must have had alternative means of hunting larger prey. There is much evidence that endurance running capabilities evolved at this time to enable *Homo* to be successful, energy-efficient, and tactful hunter and gathers (Bramble and Liberman, 2004; Liebenberg, 2008; Lieberman, 2009) It can be hypothesized that endurance running capabilities were necessary to be a carnivore and fundamental to human evolution (Liberman, 2009).

The Origin of Endurance Running Capabilities in *Homo:* Adaptation to a New Ecological Niche

Archaeological and ethnographic evidence suggest that endurance running capabilities evolved about 2 Mya as early *Homo* began to occupy a new ecological niche of social diurnal carnivores (Lieberman, 2009). Archaeological remains show that early *Homo*, particularly *Homo erectus,* had smaller teeth, larger bodies, and significant magnification in cranial capacities in comparison to *Australopithecus.* To have the body and brain size evident of *Homo erectus*, dense caloric energy and sources of sufficient amino acids would have been needed (McDougall, 2011; Bortz, 1985). Lieberman suggests that this additional energy likely came from greater quality of food, namely meat, which was obtained by means of a hunter-gatherer lifestyle. Also, the smaller teeth of *Homo erectus* could not have handled the course, rough diets of *Australopithecus* and are another indication that early *Homo* were eating processed, cooked, meat (Liberman, 2009).

What is curious about the evidence that early *Homo* were consuming meat is that there is no evidence of any sophisticated weapons at that time. The only weapons that have been uncovered and dated to 2 Mya are untipped spears which would hardly injure a large prey animal in a close encounter hunt (Liebenberg, 2008). Spears date back to only 200,000 years ago and bows and arrows to only 50,000 years ago (McDougall, 2011). How then were early humans, who were comparatively weak and slow, able to kill their prey and compete with other carnivores? It is suggested that endurance running might have allowed them to run long distances to secure carcasses, and, also, kill animals on their own by the use of what is now labeled persistence hunting (Carrier, 1984; Bramble and Lieberman, 2004) Endurance running, defined as "the ability to run long distances (>5km) using aerobic metabolism," is rare among mammals and exclusive to humans among primates (Lieberman and Bramble, 2007). Moreover, the ability to run long distances in hot, arid conditions is unique to humans and likely gave early *Homo* an immense advantage when competing with other carnivores. In the hot, open habitats of Africa, *Homo* may have been able to run their prey to death by chasing them down, keeping them above the trot-gallop transition speed and driving them into hyperthermia (Liberman and Bramble, 2007). The appearance of derived features beneficial to endurance running, correlated with a major increase in encephalization in early *Homo,* leads to the hypothesis that "endurance running evolved in *Homo* for scavenging… [and] hunting [which] suggests that endurance running may have made possible a diet rich in fats and protein thought to account of the unique human combination of large bodies, smaller guts, big brains, and small teeth" (Bramble and Lieberman, 2004). Therefore, the derived ability of endurance running of early *Homo* may have been pivotal to the survival of the genus and the evolution of the modern human morphology (Bramble and Lieberman, 2004).

Transition to fill the niche of a social diurnal carnivore gave way to an energetic positive feedback loop that was likely crucial to the evolution of *Homo* (Lieberman, 2009; Bortz, 1985). Hunting and gathering would have favored selection of cognitive and social skills, as well, as athleticism and endurance (figure 1). These skills allowed hunters and gatherers to get more food, and this increase in energy availability in turn selected for hunters and gatherers with said skills. As Bortz states, "interplay between movement and nutrition is a central theme of nature." The two major behavioral divergences from our great ape ancestors are meat-centered diets and high levels of endurance exercise. "These changes constitute a positive feedback loop which is self-perpetuating. These two features, mutually complementary, are proposed to have contributed substantially to the two major discriminatory characteristics of *Homo sapiens;* our brain and our adaptability" (Bortz, 1985). Selection for better hunting and gathering abilities led to increased available energy, which was especially important for lactating mothers, and this led to increases in reproduction rates and somatic investment, growth, and maintenance. Great reproduction rates and somatic investment then lead to increases in population, body size, and brain size which allowed for greater athletic and cognitive abilities thus continuing the cycle (Lieberman, 2016). The increase in cerebral volume was particularly significant. In evolutionary history, no organ has grown as quickly and dramatically as the human brain. Over each 100,000-year span of known human ancestral life, cerebral volume increased on average 20 cubic centimeters. The modern human brain is made up of 100 billion cells, has more than 10^{14} synapses, and receives 20 percent of the body's blood supply despite accounting for only 2 percent of body weight (Bortz, 1985). Running likely not only allowed early *Homo* to obtain the nutrition needed to nourish this brain growth but, also, itself stimulated enlargement. Exercise triggers increased secretion of the catecholamines adrenaline and noradrenaline which are strong natural stimulants. It has also been shown to increase the conversion of amino acids phenylalanine and tyrosine into catecholamines and tryptophan into serotonin. Lastly, exercise promotes increased secretion of endorphins which may have helped hunters endure the pain of running in the pursuit of food because endorphins inhibit pain signals (Bortz, 1985).

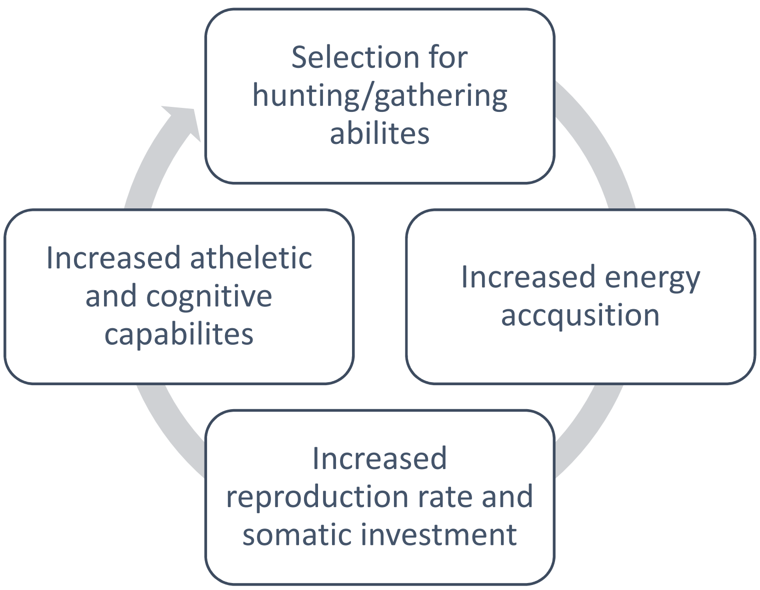

Figure 1: Endurance running gave way to an energetic positive feedback loop that was crucial to the evolution of physical and cognitive abilities needed to be successful hunters and gatherers (adapted from Liberman, 2016).

When the first *Homo sapiens* emerged, they competed with a parallel species, *Homo neanderthalensis* (McDougall, 2011). Fossil evidence shows that Neanderthals were more muscular and had denser bones, better natural insulation, and larger brains. They originated nearly two hundred thousand years before *Homo sapiens,* and in many ways, would have appeared to be the superior species. However, within ten thousand years of the origin of *Homo sapiens*, the Neanderthals disappeared. Numerous scientists think that there must have been some 'X-factor' that gave *Homo sapiens* a significant survival advantage. However, pinpointing that advantage is difficult because Neanderthals seem to have been stronger and smarter. Bramble, Carrier, and Lieberman (Carrier, 1985; Bramble and Lieberman, 2004) hypothesis that the 'X-factor' was running. Perhaps Neanderthals were too muscular and adaptions of *Homo sapiens*, particularly a slimmer body, allowed for improved endurance running capabilities. Such adaptations would have been selected for as the habitat of these two *Homo* species continued to change (McDougall, 2011). While Neanderthals were hunting larger game like bears, bison, and elk using tactics of ambush and combat, *Homo sapiens* were running down antelope. Another difference was that *Homo sapiens* ate large amounts of roots and fruit in addition to leaner meat, while evidence shows that Neanderthals only consumed rich meat. This was not a disadvantage to Neanderthals for thousands of years, but when the climate started to warm again about 45 thousand years ago, forests shrank, and grasslands grew. The more open environment made ambush hunting tactics harder for Neanderthals, and the big game they consumed retreated into the diminishing forests. The climate change, however, was ideal for persistence hunting and the growth of roots and fruit. Neanderthals became unable to hunt enough food, and with the increasing temperatures, were unable to adopt persistence hunting strategies because of their abundant muscle and greater body weight. Endurance running would have been more difficult and costly for Neanderthals, and it would have been much harder for them to maintain heat balance. Therefore, with the warming climate, the slimmer *Homo sapiens* outcompeted the more robust Neanderthals (McDougall, 2011).

Biomechanics of Bipedalism: Adaptations for Walking Versus Running

There are significant mechanical differences between walking and running that are relevant to the discussion regarding the role endurance running had on human evolution. Walking uses an inverted pendulum mechanism in which kinetic energy and potential energy are exchanged out of phase with each step (figure 2). The mechanism consists of three phases: heel-strike, midstance, and toe-off. During heel-strike, the heel of one foot strikes the ground while the other foot lifts. Forward kinetic energy is exchanged for potential energy between heel-strike and midstance. The head and center of mass reach their highest points when the legs are relatively straight; one in contact with the ground and the other just about to land. This is mid-stance. The hovering foot then contacts the ground while the toe of the other foot lifts, vaulting the center of mass over the extended leg, where it is at its lowest point, and exchanging potential energy for kinetic energy (Bramble and Lieberman, 2004; Novacheck, 1998). The metabolic cost of transport (COT) for walking produces a U-shaped curve (figure 2) with an average optimal speed of about $1.3 ms^{-1}$. The optimal speed for a given person, however, varies as a function of leg length (Alexander, 1980). At about $2.3\text{-}2.5 ms^{-1}$, most humans voluntarily start to run because running at this speed is less costly than walking, corresponding to the point the COT curves for walking and running intersect (Margaria, 1963; Alexander 1991).

Running uses a mass-spring mechanism which exchanges potential energy and kinetic energy differently than in the inverted pendulum mechanism of walking (figure 2). During the three components of the running stride - foot-strike, mid-stance, and toe-off- kinetic energy, and potential energy are in phase, unlike walking in which they are out of phase (Novacheck, 1998). One foot strikes the ground, foot-strike, while the other foot lifts, and both kinetic energy and potential energy decline. The center of mass reaches its lowest point at mid-stance during which leg tendons and ligaments partially convert the decrease in kinetic energy and potential energy into elastic strain energy. The foot in contact with the ground then lifts before the other foot lands during which the body is in an aerial phase. The center of mass is the highest at this point. In the transition from the aerial phase to toe-off, the stored elastic strain energy is released through recoil propelling the body forward (Bramble and Lieberman, 2004).

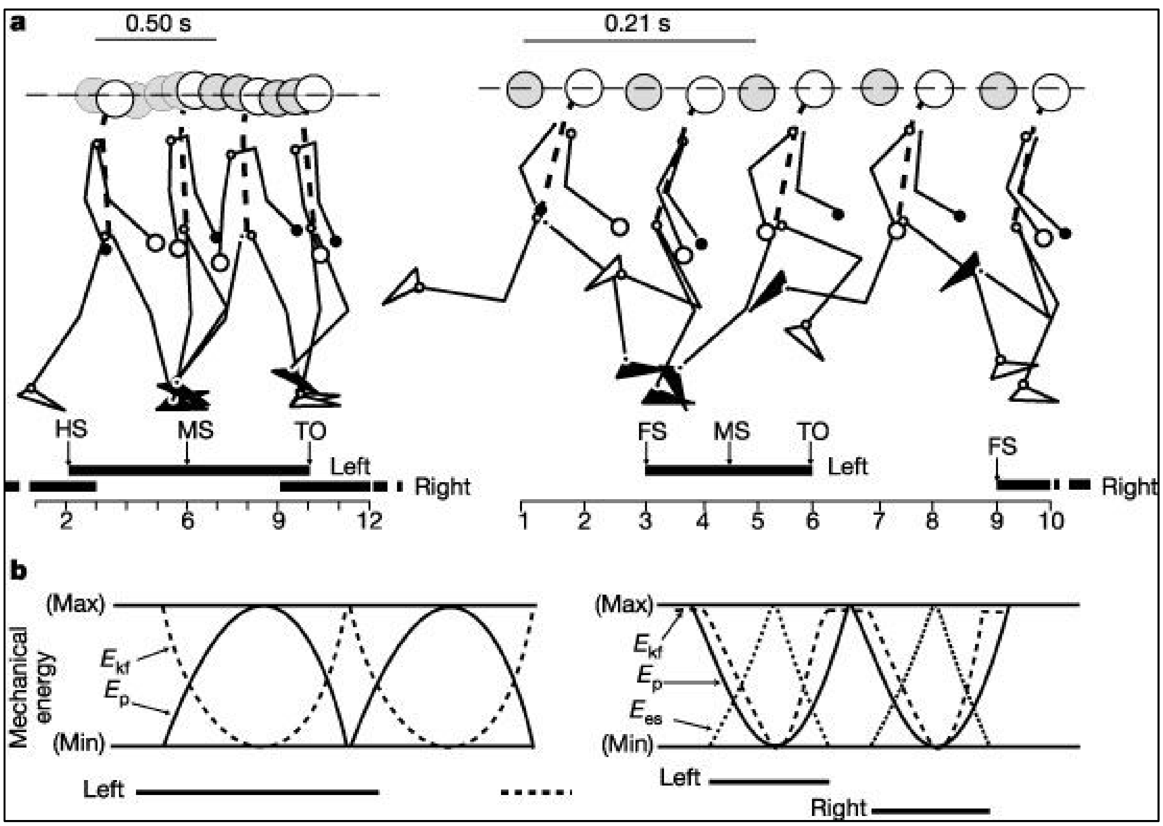

Figure 2: Walking utilizes an inverted pendulum mechanism during which kinetic and potential energy are exchanged out of phase through use of a compliant limb. Running utilizes a mass-spring mechanism during which kinetic and potential energy are exchanged in phase by use of energy storing tendons in the lower limbs. The COT curves for walking and running are 'U' shaped and the point where they intersect in when running is more energetically efficient than walking at the same pace. *Source:* Bramble and Liberman (2004)

Many derived features of *Homo* that are crucial to the mass-spring mechanism of running appear to have little or no role in the inverted pendulum mechanism of walking, suggesting that such features were adapted for the purpose of running and are not just byproducts of adaptations for bipedal walking (Bramble and Lieberman, 2004). A study by Bramble and Lieberman (2004) examined the anatomical and physiological specializations key to human endurance running, and the extent to which these structures evolved originally for bipedal walking or independently for bipedal running. They organized features of the human skeleton with cursorial functions by their functional role and whether they benefit both walking and running equally, benefit running more than walking, or are biomechanically specific to running and thus functionally unrelated to walking. Only one feature, long legs, appeared to benefit walking and running equally. Of the other 31 features examined, 15 were found to play a larger role in running than walking, 15 were specific to running, and one was inconclusive (figure 3). Bramble and Lieberman argue that even though some of the derived features are beneficial to walking, walking alone cannot account for all the features. Features specific to the mass-spring mechanism of running such as a balanced head, short toes, short femoral necks, stabilizing plantar arches, the nuchal ligament, a system of springs in the legs and feet, a larger gluteus maximus, spinal extensor muscles, an elongated, narrow waist, and a low, wide decoupled shoulder girdle are vital to running but play little to no role in walking (figure 4) (Bramble and Lieberman, 2004; Lieberman, 2009). In addition, long-distance running has mechanical and thermoregulatory challenges beyond those experienced during distance walking. While, certain mechanisms to reduce stress on the skeletal system and release excess heat, such as larger joint surfaces, sweating, and hairlessness, are beneficial to walking, they are essential to the ability to run long distances. Therefore, it is reasonable to conclude that human endurance running capabilities are not simply a byproduct of bipedal walking or an aberrant behavior but have deep roots in the evolution of humans. Further research and more extensive fossil evidence are needed, however, to determine if walking and running co-evolved or if walking evolved first and then running evolved later (Bramble and Lieberman, 2004).

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.

Figure 3: Most derived features of the human skeleton with cursorial function are specific to running or play a larger role in running than walking indicating that bipedal running evolved independently from bipedal walking and not merely as a byproduct. *Source:* Bramble and Lieberman (2004)

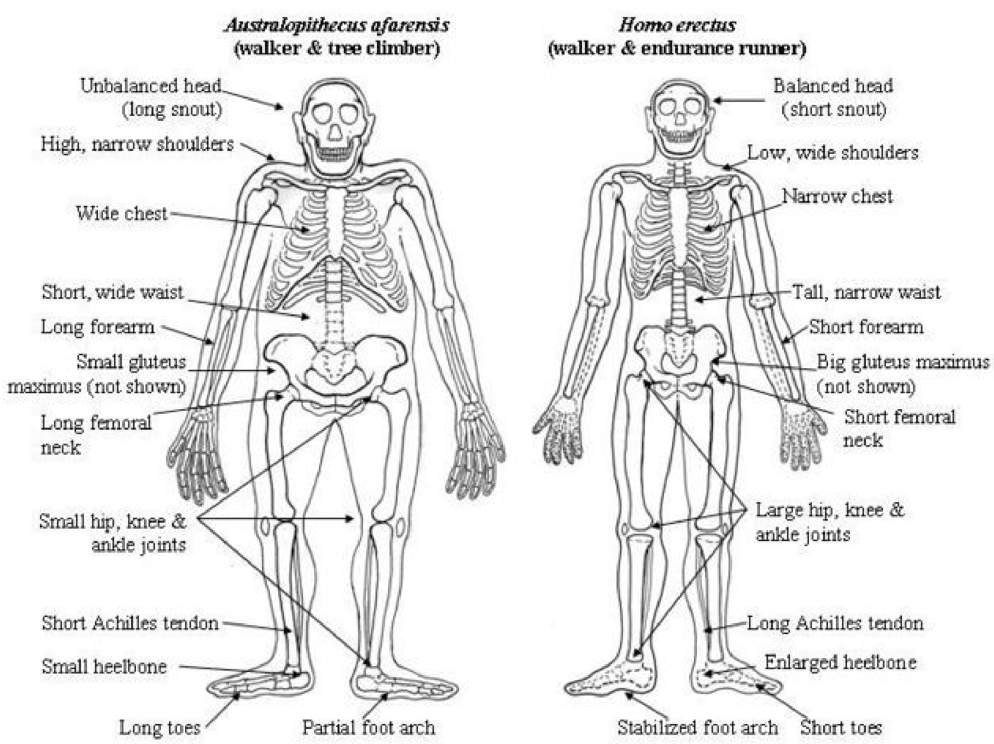

Figure 4: Many derived features of *Homo erectus* that differ from *Australopithecus afarensis* were adapted for endurance running abilities. *Source:* cogweb.ucla.edu

Overcoming the Physical Demands of Endurance Running: Derived Features of *Homo*

When compared to other cursorial mammals, mammals with limbs adapted for running, humans are often considered poor runners (Bramble and Liberman, 2004). The human sprint is much slower than the gallops of other mammalian cursorial species. Running demands about twice the metabolic energy for humans that it does for other mammals of equal body mass (Taylor et. al., 1982). Humans are also less maneuverable and lack elongated digitigrade feet, feet structured so the animal walks on its toes, and short proximal limb segments that benefit quadrupedal cursors (Bramble and Lieberman, 2004). What humans have that other cursors do not is the ability to run long distances using aerobic metabolism-endurance running (Liberman and Bramble, 2007). Derived specialized anatomical, physiological, and behavioral features evident in the *Homo* genus, but absent in earlier ancestors, allow humans to store and release energy in the lower limb, stabilize the body's center of mass, and overcome thermoregulatory constraints when running long distances (Liberman and Bramble, 2007). In comparison to other primates, running capabilities are exclusive to humans. Other primates, such as our closest ancestor the chimpanzee, are poor runners and do not rely heavily on running. This is partly due to anatomical features such as large hands and feet and short forelimbs that are specialized for climbing trees but hinder the ability to run. When compared to other cursorial mammals, humans are also unique. Most cursorial mammals are good sprinters because they need speed to escape a predator or catch a prey. They, however, cannot sustain this speed, known as the gallop gait, for a long period of time without overheating. Humans, despite being relatively slow and lacking the ability to gallop due to bipedal locomotion, can run long distances without overheating with a gait mechanically similar to quadrupedal trotting. There are four major limiting biomechanical and physiological demands of endurance running that *Homo* were able to overcome: energetics, stabilization, strength, and thermoregulation (Bramble and Lieberman, 2004).

Regarding energetics, humans have musculoskeletal specializations for bipedalism. Bipedal running in humans is energetically efficient because it utilizes a mass-spring gait. Anatomically, this mass-spring mechanism relies on the many tendons in human legs and feet, namely the Achilles tendon and iliotibial tract (Lieberman and Bramble, 2007). Many of these spring-like tendons are unique to humans among primates and are hypothesized to have been absent in *Australopithecus* and originated early in the *Homo* genus along with other anatomical structure relevant to running. Arguably, the most important of these energy-storing springs is the Achilles tendon which is longer in *H. sapiens* than they were believed to have been in *Australopithecus* or are in modern chimpanzees (Lieberman and Bramble, 2007) Another important set of springs is the plantar arch which has two major functions important to running. First, it helps keep the medial tarsals rigid to provide power at toe-off. It also absorbs some impact after heel strike and acts as a spring, returning energy generated during each stance phase (Ker et.

al., 1987). Analysis of australopithecine foot bones suggests that they had only a partial arch like that in modern chimpanzees (Bramble and Lieberman, 2004).

Another feature of human endurance that is energetically favorable, and differs from most quadrupeds, is that humans increase speed mostly by increasing stride length rather than rate (figure 5) (Alexander et. al., 1980) While speed is a function of both cadence, stride rate or turnover, and stride length, increases in cadence are only significant below and above the endurance range. Within the endurance range, about 2.5-6.5 meters per second, cadence is largely independent of stride length so speed can be increased without significantly increasing stride rate (Lieberman, 2018). Cavanagh and Kram (1989) found that stride length increases by approximately 26% between the speeds of 3.15ms^{-1} and 4.12ms^{-1} while stride rate increases by only 4%. Because humans have long legs equipped with many energy-storing springs, humans can take longer strides relative to their body mass than similar-sized quadrupeds. Quadrupeds must compensate for their shorter legs by increasing cadence to increase speed which is more energetically costly (Bramble and Liberman, 2004). Longer strides increase contact time with the ground which is beneficial because steps are costly (Kram et. al., 1990). The more steps that are taken, the more energy is used (Alexander, 1980). Energy consumption, as measured by the submaximal rate of oxygen consumption (VO_2), is inversely proportional to the time the foot applies force to the ground during each stride which increases with ground contact time. Therefore, energy consumption is equal to body mass divided by ground contact time (Kram and Taylor, 1990). Long legs relative to body mass originated unequivalently in *Homo erectus* but could have also been relevant to earlier species of the *Homo* genus (Aiello et. al., 1990). These longer legs also make up less of the total body mass than they did in earlier hominids (Bramble and Lieberman, 2004). Modern humans have more compact feet and shorter toes than australopithecines. Since oscillating legs create energetic costs proportional to the leg’s mass moment of inertia, a decrease in distal limb mass equates to significant metabolic savings (Bramble and Lieberman, 2004).

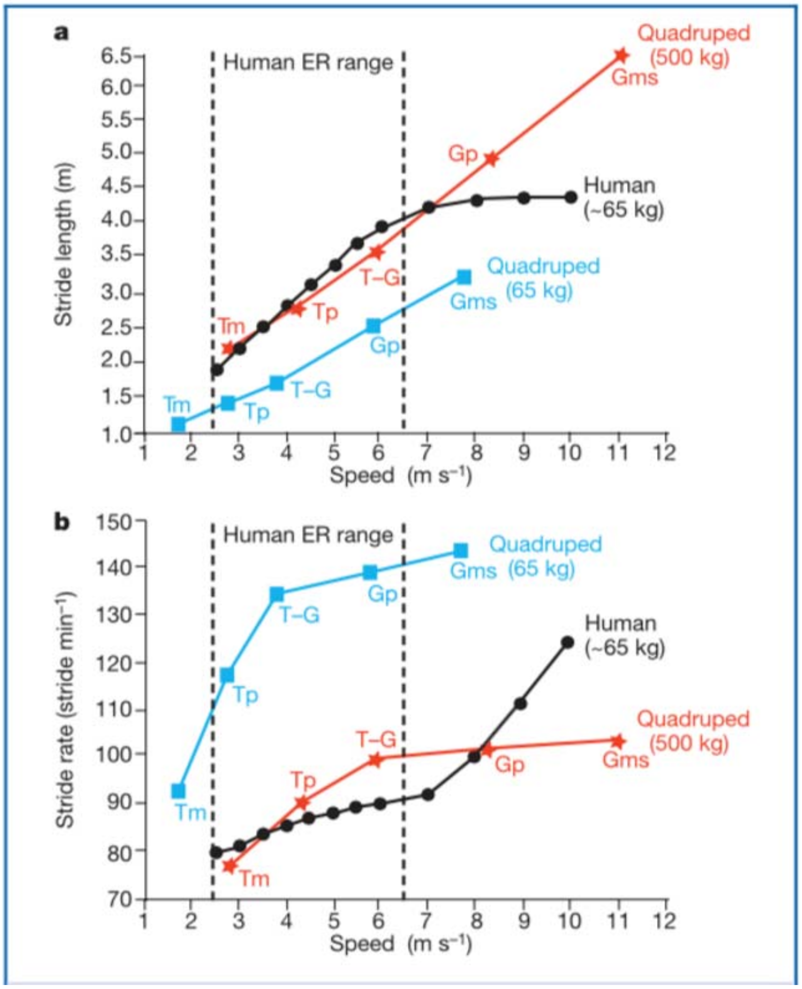

Figure 5: Humans can increase speed within the endurance running range largely by increasing stride length with little change to stride rate. This allows for humans to increase speed at less of an energic cost compared to similar-sized quadrupeds which have shorter stride lengths and faster stride rates at comparable speeds. *Source:* Bramble and Lieberman (2004)

Considering stabilization, bipedal gaits are inherently more unstable than quadrupedal ones, and the more pronounced forward inclination during running makes it more unsteady than walking (Bramble and Lieberman, 2004). Humans, however, have many derived features that help stabilize that center of mass of the trunk and head while running (Lieberman and Bramble, 2007; Aiello et. al., 1990). Members of the *Homo* genus have expanded areas on the sacrum and posterior iliac spine for erector spinae muscles to attach to and a larger transverse process of the sacrum which helps stabilize the sacroiliac joint. Also, to accommodate this inherent instability, humans have evolved a larger gluteus maximus which enhances trunk stabilization while running. During the walk, one foot is always on the ground which allows abductors and medial rotators of the stance hip, the one ipsilateral to the foot on the ground, to counteract trunk rotation caused by the forward movement of the swing leg, the one not in contact with the ground. While running, however, the body cannot counteract rotation in this way because there is not always one foot on the ground. While running the torques created by forward acceleration are counteracted by torques created by counter-rotation of the thorax and arms (Hinrichs, 1990). Three derived features in the hips and shoulders allow humans to generate these opposing torques. The first is an elongated narrow waist which allows greater isolation of trunk rotation by separating the lower thorax from the pelvis (Aiello et. al., 1991). The second is decoupling of the head and the pectoral girdle which allows for independent counter-rotation of the pectoral girdle and arms without much axial rotation of the head. The third is wider shoulders and reduced forearms which allow that arms to swing which acts as a counterbalance. Also, reduced mass of the forearm makes it easier to keep a flexed elbow while running (Bramble and Lieberman, 2004). The final challenge to stability while running is the tendency of the head to pitch forward during foot strike due to its vertical orientation (Bramble and Lieberman, 2004; McDougall, 2011). Three more features seen in *Homo* relative to *Australopithecus* or *Pan* are decreased facial length, occipital projection behind the foramen magnum, and larger semicircular canals. Larger semicircular canals allow for greater sensitivity of the vestibulo-ocular reflexes to rapid pitching movements, and, thus, increase sensitivity to head pitching in the sagittal plane (Bramble and Lieberman, 2004; Lieberman and Bramble, 2007; Aiello et. al., 1990).

The third demand of endurance running is skeletal strength which is important because running puts significant stress on the skeletal system; much more so than walking (Bramble and Lieberman, 2004). Each time the foot meets the ground, a shock wave passes from the heel through the spine to the head. Vertical ground reaction forces can reach up to four times the runner's body weight (McDougall, 2011). Some of this stress is reduced by limb compliance and mid-foot striking which allow elastic strain energy to be stored in the lower limb tendons. Larger joint surface areas in the lower limb, not matched in the upper limb (Jungers, 1988), also help spread forces over larger areas and reduce the stress to any one joint. Members of the *Homo* genus have larger articular surface areas than *Pan* and *Australopithecus*. In addition to larger articular surface areas, humans, beginning with *H. erectus*, have larger iliac pillars which allow the pelvis to resist the stress of running (Aiello et. al., 1990). The shorter femoral necks in humans as compared to *Pan* and *Australopithecus* may also benefit running by reducing bending movements in the femoral neck and thus minimizing angular momentum in the trunk (Bramble and Lieberman, 2004; Hinrichs, 1990).

The major limitation to other cursors, when is come to endurance running, is their inability to sustain fast speeds without overheating. Humans have a unique thermoregulatory mechanism that allows them to cool their core body temperature effectively while maintaining endurance speeds. This trait is not seen in any other cursors, primates, or early hominids. The mechanism used to release mass amounts of body head is sweating, and this is what gives humans such a great advantage in hot, arid conditions. With many more eccrine sweat glands for a given surface area than other mammal, humans can quickly dissipate heat by evapotranspiration (Lieberman and Bramble, 2007). Additionally, their reduced body hair and narrow, elongated body forms increase convection rates (Ruff, 1990). Mouth breathing, rather than panting, is another advantage because it is not only a good means of releasing heat, but it also allows for greater airflow with less resistance and muscular effort (Bramble and Lieberman, 2004).

Integration of Respiration and Locomotion: Implications for Running

A major constraint on running in all mammals is the ability to breathe while maintaining a run. Quadrupedal mammals, with the function of their respiratory system closely integrated with locomotion, are limited in the distance they can travel at a certain speed (McDougall, 2011). "When many quadrupeds run, their internal organs slosh back and forth like water in a bathtub. Every time a cheetah's front feet hit the ground, its innards slide reward, sucking air back in" (Bramble; direct quote from McDougall, 2011). For this reason, quadrupedal animals take just one breath per stride. The only cursorial mammal that is not limited to one breath per stride is humans. Humans usually use a 2:1 breath to stride ratio but can also employ several others (Bramble and Carrier 1983). Humans have this ability because their internal organs do not move as much with running, and they release most of their heat by sweating opposed to panting like all other cursorial mammals (McDougall, 2011).

David Carrier (1983) was the first to hypothesize that the human body adapted for improved respiration mechanisms. Perhaps bipedalism evolved, in part, for greater ease of respiration during locomotion, and this improved respiration played a major role in humans' endurance running abilities. Carrier first came across this idea while dissecting a jackrabbit. He noticed that the muscles on the diagram of the jackrabbit were not strongly anchored down to the lumbar vertebra like they are in the abdomens of other mammals. The muscles were instead attached to the flimsy abdominal bones, and they sprang back when compressed. Jackrabbits run the same way that all other quadrupedal mammals do, arching their backs with each stride. "When they push off with their hind legs, they extend the back, and as soon as they land on the front legs, the back bends dorsally" (McDougall, 2011). Carrier hypothesized that jackrabbits have spring-loaded abdomens while other mammals, such as big cats which hunt rabbits, do not, because the jackrabbit needs to be faster, for at least a short period of time, for the species to survive. If the jackrabbit's predator, for example, a mountain lion, could run at the same speed as the jackrabbit, then the lion would always catch the jackrabbit, and the jackrabbit population would die out. This would then cause the predator population to die out due to lack of food. The springs may allow the jackrabbit to run faster for a short period of time by helping it breathe in a way the predator cannot. Muscles need oxygen to convert food to energy that the animal needs to be able to exchange gases to sustain top speed. The abdominal springs in the jackrabbit act like levers allowing the jackrabbit to pump air in and out of its lungs just a little bit faster than the predator (McDougall, 2011; Carrier et. al., 1984). Carrier found that jackrabbits can run up to forty-five miles per hour, but due to the high energy consumption of doing so, can only maintain that speed for half of a mile, about 45 seconds. Most predators of jackrabbits can only run up to forty miles per hour but can sustain that speed for much longer. What this implies is that jackrabbits have about 45 seconds to find safety before they are caught by a predator in pursuit (McDougall, 2011). The greater flexibility of the abdominal muscles in the jackrabbit gives it the vital advantage of enhanced respiration with locomotion. Perhaps humans stood upright to improve respiration mechanisms by reducing strain on the lungs and allowing for greater flexibility of the abdominal muscles, thus permitting humans to breath more effectively while running (Carrier et. al., 1984).

A set of experiments by Bramble and Carrier (1983) examined synchronization patterns between gait and breathing in running mammals. Subjects included several quadrupeds and humans, bipeds. Bramble and Carrier thought that perhaps the reduction of mechanical constraints on respiration from the evolution of a bipedal gait, namely absence of subjection of the thoracic complex to direct impact loading, meant humans did not need to synchronize their breathing and gait during sustained running like quadrupedal cursorial mammals do. Results, however, showed that integration of respiration and locomotion is required in both quadrupeds and bipeds to effectively ventilate the lungs and maintain aerobic metabolism (figure 6). A difference is apparent, though, in the patterns of synchronization, indicating that bipedalism does give humans a large advantage when it comes to breathing while running. A constant ratio of 1:1 strides per breath was seen in all quadrupedal species tested (jackrabbits, dogs, horses) at both the trot and the gallop. Human subjects, however, employed multiple phase-locked patterns (4:1, 3:1, 2:1, 1:1, 5:2, and 3:2). It was found that a 2:1 coupling ratio was favored (figure 6). A 4:1 ratio was seen often in more experienced runners at slow sustained speeds, and a 1:1 ratio was only seen when running uphill or downhill (Bramble and Carrier, 1983). The wide range of locomotor-respiratory coupling ratios available to human runners is beneficial because, at any stride frequency, the human's respiratory rate can be much lower than a quadruped. Humans can also increase speed and alter their breathing pattern without changing gait which might help humans regulate energetic costs (Bramble and Carrier, 1983).

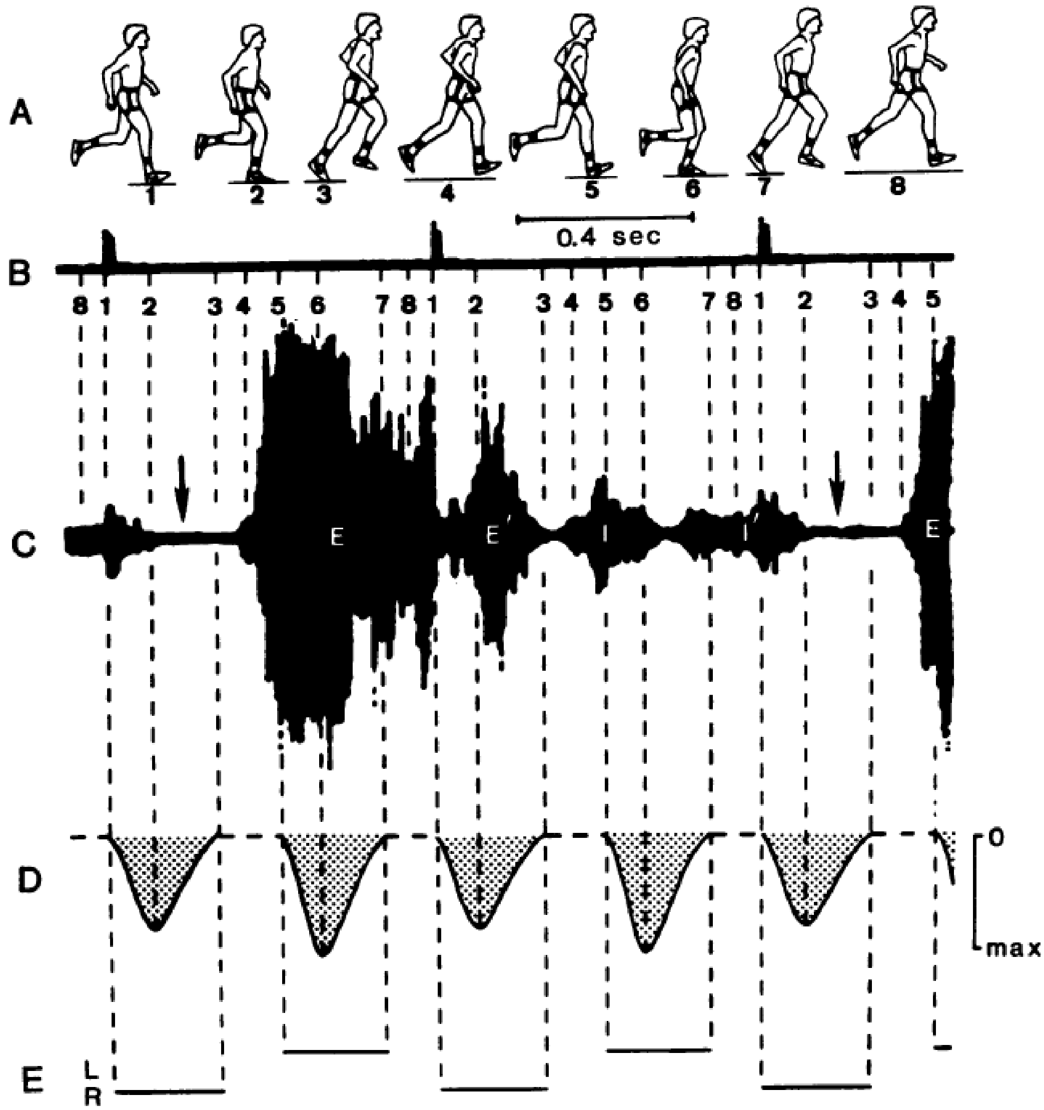

Figure 6: Experiments shows that synchronization of breath and locomotion is necessary for humans while running. Differing from quadrupedal subjects which preferred 1:1 coupling ratio, human subjects favored a 2:1 ratio. *Source:* Bramble and Carrier (1983)

In addition to adaptations for improved mechanical mechanics of breathing while running, selection may have acted for the evolution of greater oxygen carrying capacities in humans. Physiologists have found that humans must exercise strenuously at least three times per week for at least 30 minutes to achieve an optimal VO_2 max, the maximum amount of oxygen one can utilize during maximal aerobic activity (med.virginia.edu). This pattern of exercise aligns with the physical activity of modern hunters and gathers. Bortz suggests that the oxygen-carrying capacity of modern humans, structural and functional, evolved as an integral component of early humans' hunting and gatherer lifestyle (Bortz, 1985).

Persistence Hunting and The Endurance Running Hypothesis

The unparalleled ability to run long distances without overheating is likely what made primitive humans successful predators. Mammals, including humans, can only tolerate an increase of 6-7°C of their core body temperature. Exceeding 44°C causes structural and functional changes to occur that lead to death by hyperthermia (Bortz, 1985). The metabolic heat produced when running, in addition to ambient heat, leads to hyperthermia quickly in most cursorial mammals. Humans uniquely differ in that they can dissipate heat much more efficiently due to their greater ability to sweat and lack of body hair. Most other mammals, while many sweat to a degree, rely primarily on panting to release body heat and running fast puts a mechanical limitation on this cooling mechanism (Bortz, 1985). Therefore, most quadrupedal cursorial mammals can only sustain a gallop for 10-15 minutes before they must slow to a trot (Bramble and Lieberman, 2004).

Biomechanically, human bipedal running is like quadrupedal trotting. Both synchronize the contralateral forelimbs and hindlimbs which restricts the stride cycle to two steps and creates significant vertical displacement of the center of mass. The two gaits are also comparable in speed (Bramble and Lieberman, 2004). Although the quadrupedal gallop is much faster than the bipedal sprint, the typical endurance speed for humans exceeds the trot-gallop transition speed of other mammals, regardless of size (figure 6). Therefore, over longer distances, such as the marathon, in which other mammals are restrained to a trot by thermoregulatory limitations, humans are faster and can outrun nearly all other mammals, even horses. The ability of humans to outrun other mammals increases in hot, arid conditions in which mammals lacking the thermoregulatory mechanisms of humans, overheat faster and have a greater potential for hyperthermia (Liberman and Bramble, 2007). Such hot, arid conditions are believed to be consistent with habitats of early *Homo* in which the origin of endurance running capabilities is evident (Liebenberg, 2008).

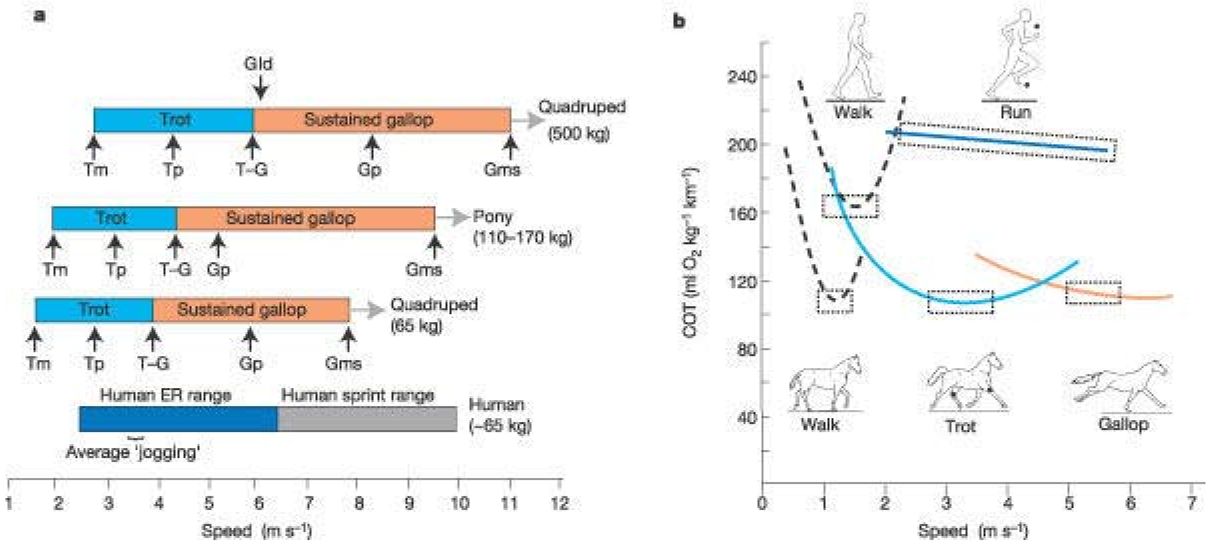

Figure 6: a. Human endurance speeds exceed the trot gallop transition of many quadrupedal mammals which is fundamental to persistence hunting. **b.** The run COT curve for human has a wider range of optimal speed than for the trot and gallop in horses.

The difficulty of providing evidence to support the persistence hunting hypothesis is that such a method of hunting leaves behind no weapons or skeletal evidence (Liebenberg, 2008). The work of Liebenberg (2008) provides support that persistence hunting is a possible and effective means of hunting. He conducted anthropological research with the Bushmen of the Kalahari Desert and witnessed them perform persistence hunts. Liebenberg recalls the skill and cooperation of the hunters he observed. The hunters begin tracking a kuda, a species of antelope, herd at a walk. When they find the herd, they break into a run, targeting a single kudu, driving it out of the shade, and cutting it off from the rest of the herd. Some men conduct the pursuit as others analyze the tracks to make sure the same kuda is being pursued the whole time and that the running hunters do not display tracks that indicate that they are over-exhausted. The strongest man of the group holds back, supplies water to the runners, and saves himself for the end of the hunt when more speed is needed. He does not step in until the kuda's tacks indicate that it is severely overheated and on the edge of hyperthermia (McDougall, 2011). After witnessing several persistence hunts, in addition to bow and arrow hunts, Liebenberg learned that persistence hunts are more effective. "Only a small percentage of arrow shots are successful, so for the number of days hunting, the meat yield of a persistence hunt is much higher" (McDougall, 2011). Liebenberg also noticed that the Bushmen maintain a different diet than most modern humans as a result of their hunter and gatherer lifestyle. They never know when they will need to pursue a hunt so they graze slightly throughout the day to keep up their energy and hydration without filling up to the point that they would not be able to run. Lastly, Liebenberg found that, despite the hypothesis of Bramble and Lieberman (2004) that persistence hunting requires hot temperature, the Bushmen of Kalahari continue to successfully use the tactic in all weather conditions (Liebenberg, 2008; McDougall, 2011).

Running and the Evolution of Neurobiology

The magnification of the brain in early *Homo* species could be linked to the evolution of endurance running capabilities in humans. The human brain has grown to be seven times larger than any comparable mammal, and the brains of *Homo sapiens* use 20 percent of the bodies energy even though it accounts for only two percent of body weight (Bortz, 1985). Chimpanzees, on the other hand, have brains that use nine percent of their energy intake (McDougall, 2011). It is clear that humans started eating meat about 2 million years ago due to the magnification of the brain that would have necessitated reliable sources of food with high concentrations of calories, fat, and proteins (McDougall, 2011). As endurance abilities of early *Homo* advanced, brain size increased. Perhaps brain size is tied to physical capability (Raichlen and Gordon, 2011). It is possible that running capabilities allowed earlier humans to obtain meat needed to fuel the growth of their brain, and that enlargement of the brain, and thus the head, improved running abilities. "The human head, with its unique position directly on top of the neck, acts like the roof weights used to prevent skyscrapers from pitching in the wind. Our head didn't just expand because we got better at running… we got better at running because our heads were expanding, thereby providing more ballast" (Lieberman, 2009). The head, counterbalanced and kept aligned by the arms, helps prevent the torso from twisting midstride, and makes running more efficient (McDougall, 2011).

In a 2013 study, Raichlen and Polk hypothesized that the increases in aerobic activity of early humans when they adopted the new niche of hunters and gatherers may have contributed to the magnification of the brain and improvement of cognitive function. Positive correlations have been seen between aerobic physical activity and the production of new neurons, increase in brain structures, and advanced cognition in humans and other mammals (Raichlen and Polk, 2013). Running, which was a necessary capability to obtain meat needed for brain growth, may have also been a crucial factor in itself. Major cranial growth was first evident in *Homo erectus* (Bramble and Lieberman, 2004). It has been hypothesized that this increase in brain size was a result of increased cognitive demands (Holloway, 2008), but more recently, Raichlen and Polk suggested that endurance running, needed to be competitive hunters, also played a role. They hypothesized that "selection acting on human locomotor endurance has a measurable effect on the evolution of human brain structure and cognition" (Raichlen and Polk, 2013). Exercise has been shown to increase the size of different brain components and improve cognitive abilities in humans. Studies have shown correlations between physical capability and brain size in many mammals, especially with the expansion of the hippocampus which is linked to improved memory (Raichlen and Gordon, 2011). Perhaps, "selection acting on endurance increased baseline neurotrophins and growth factor signaling (compounds responsible for both brain growth and for metabolic regulation during exercise) … which in turn led to increased overall brain growth and development" (Raichlen and Polk, 2013).

Multiple studies using rats as a model organism suggest that aerobic physical activity stimulates neurogenesis in the hippocampus, frontal cortex, and motor cortex (Praag, 2008; Praag et. al., 1999). In studies with human subjects, aerobic fitness has been compared to the size of different brain components. Results show that aerobic fitness is positively correlated with hippocampal and basal ganglia volume and the density of grey matter in the insula and frontal lobes. Greater levels of aerobic activity have also been linked to greater cognitive function in children and adults (Erickson et. al., 2001; Peters et. al., 2009). Such physical activity likely leads to greater neurogenesis and cognitive abilities through upregulation of neurotrophins and growth factors. A neurotrophins that has been found to increase with running in both rodents and humans is brain-derived neurotrophic factor (BDNF). Two growth factors that increase with physical activity are insulin-like growth factor I (IGF-1) and vascular endothelial growth factor (VEGF). Both growth factors enhance neurogenesis (Raichlen and Polk, 2013). Levels of circulating IGF-1 and VEGF are greater in humans who have been undergoing long-term endurance training, indicating that the effects of aerobic physical activity on neurogenesis is sustained over time. BDNF, IGF-1, and VEGF also impact metabolic pathways which in turn improves aerobic performance in a positive feedback loop. IGF-1 and VEGF "stimulate tissue and vascular system growth and repair, which improves oxygen delivery to muscles and increases aerobic performance… BDNF and IGF-1 facilitate lipid oxidation in muscles and glucose metabolism, which are essential for energy regulation during submaximal activity" (Raichlen and Polk, 2013). With these positive feedback loops at play it is possible that selection for greater endurance exercise capabilities also selected for larger brains because physical activity stimulates pathways that cause neurogenesis, greater energy regulation, and vascular (Raichlen and Polk, 2013).

Studies of several mammalian species have shown that selection on aerobic endurance ability likely affects brain size (Lieberman et. al., 2009). It is probable that humans underwent similar selection that played a major role in neurobiological evolution. Raichlen and Polk (2013) tested the hypothesis that "increased brain size during human evolution was, in part, related to a shift to higher levels of aerobic activity," by comparing two morphological traits found by Bramble and Lieberman (2004) to have adapted for endurance running performance. The two traits they examined were hindlimb length and semicircular canal dimensions because these traits could easily be compared across the great apes, humans, and hominin taxa. Longer hindlimbs increase stride length allowing for greater endurance speeds at reduced energetic costs. A more extensive semicircular canal system is also beneficial to endurance running because it allows for the sensation of angular head motion and thus improves maintenance of stability (Bramble and Lieberman, 2004). *Homo erectus* and later members of the *Homo* genus have longer hindlimbs and greater anterior and posterior semicircular canal radii than australopithecines and great apes (Bramble and Lieberman, 2004). Examination of correlations between size-corrected hindlimb lengths and semicircular canal radii and encephalization quotients in humans, great apes, and fossil hominins, yielded significant positive correlations (figure 7). "Encephalization quotients quantify the difference between observed brain size and the brain size expected for a mammal of similar body mass, and thus provide an important measurement of brain size evolution" (Raichlen and Polk, 2013). These findings indicate that brain size increased as morphological adaptations for endurance running capabilities evolved.

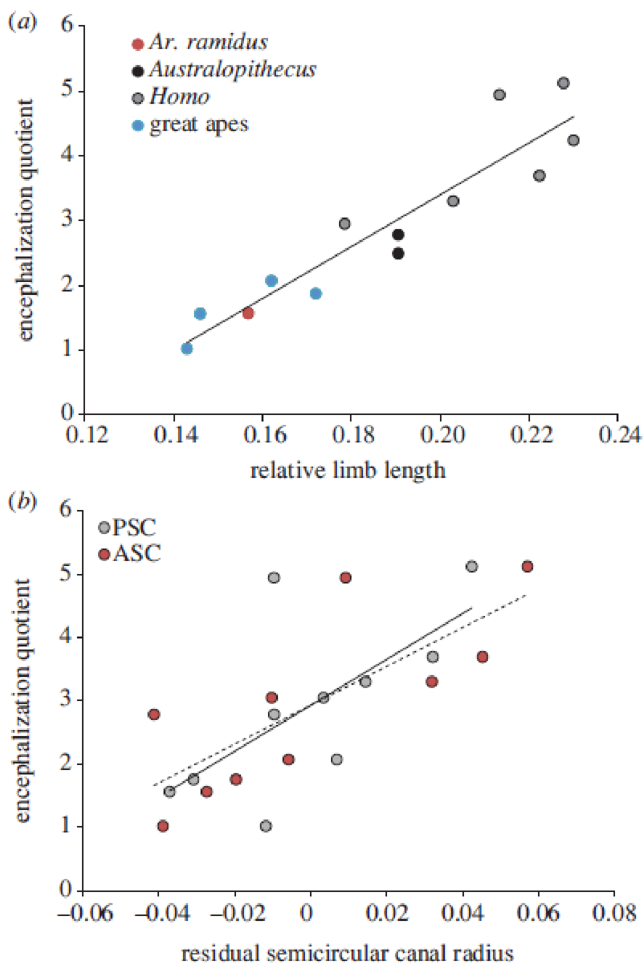

Figure 7: Encephalization quotients are positively correlated with size-corrected hindlimb length and residual semicircular canal radii in hominids, suggesting coevolution of morphological features for endurance running and brain size.

Another hypothesis regarding the evolution of the brain and running abilities is that the interaction of dopamine and endorphins acted in selection of endurance running capabilities by enhancing pleasure associated with physical activity (Raichlen and Gordon, 2011; Bortz, 1985). Running has been found to dramatically increase endorphin levels in humans (Boecker et. al., 2008). This rise in endorphins creates a feeling of euphoria. Running often involves a level of physical pain and discomfort, which was likely an obstacle to early humans that relied on running to obtain food. It is possible that the "human body evolved to release hormones associated with euphoric states so that when one is faced with a particularly trying physical feat, [such as that of a persistence hunt], the cephalic space is permeated with chemicals that induce a sense of calmness" (Schulkin, 2016).

Conclusion

The adaptation of endurance running capabilities likely played a crucial role in the survival of *Homo sapiens* and the evolution of the modern human body form. It is likely that running capabilities evolved independently from bipedal walking capabilities as shown by the numerous morphological features that are central to running but nearly irrelevant to walking (Bramble and Lieberman, 2004). The endurance running hypothesis states that early *Homo* adapted to be able to run long distances in order to fill the new ecological niche of diurnal social carnivores, demanded by climate changes and more open habitats (Lieberman and Bramble, 2007). Such capabilities allowed early humans to obtain meat, needed for the expansion of their brains, through the practice of persistence hunting (Liebenberg, 2008). Early humans utilized their unique abilities to sweat, integrate breath with locomotion, and economically increase speed by increasing stride length to drive prey into hypothermia and kill them without the use of projectile weapons (McDougall, 2011). It is likely that this lifestyle of high levels of aerobic physical activity also stimulated neurogenesis and, thus, was a major cause the magnification in cranial size evident in advancing *Homo* species (Raichlen and Polk, 2013).

The fundamental role running had in human evolution hold important implications for modern health and disease. The Tarahumara, an indigenous group living in the Copper Canyons of Chihuahua, Mexico, are known for their remarkable endurance running abilities. Even more remarkable though is that anthropologists that have studied the Tarahumara culture have noted that obesity, drug addition, abuse, heart disease, high blood pressure, diabetes, and depression are unheard of in their culture. In addition, cancer rates are barely detectable (McDougall, 2011). This is shocking given that the Tarahumara have no access to modern medicine, live in the harsh environment of the Copper Canyons, fuel from mainly beans and corn, and run high mileage daily in nothing but hand-made sandals. Also, surprising is that old age doesn't seem to slow them down. Eighty-year-olds run the same amount as middle aged and teenaged members of the tribe (McDougall, 2011).

Lieberman suggests that perhaps our modern sedentary lifestyle is driven by biological mechanism that once helped the species survive, but now harms us because we are made for high levels of physical activity. The human brain is wired to tell us to rest whenever we can and conserve energy because for much of human history doing so was necessary for survival. Humans needed to save their energy for the next hunt. However, today when food is just a walk to the fridge or trip to the grocery store, we have no need for endurance exercise. It is possible that the absence of the physical activity that was fundamental to our survival is a leading factor in many modern diseases (Lieberman, 2014). Further research on the role running had in human evolution and the implications such the effects of physical exercise on health, could be constructive in understanding and treating many modern diseases that plague developed societies.

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