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The Evolution of Marathon Running Capabilities in Humans

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Abstract

Humans have exceptional capabilities to run long distances in hot, arid conditions. These abilities, unique among primates and rare among mammals, derive from a suite of specialised features that permit running humans to store and release energy effectively in the lower limb, help keep the body's center of mass stable and overcome the thermoregulatory challenges of long distance running. Human endurance running performance capabilities compare favourably with those of other mammals and probably emerged sometime around 2 million years ago in order to help meat-eating hominids compete with other carnivores.

For years, running marathons was considered an odd and potentially dangerous activity. Indeed the tale of Phidippides, who dies from his exertions, might be considered as much of a warning as a celebration of the human ability to run 42.195km. Yet, the increasing popularity of marathon running among humans of all ages and abilities is a testament to our species' capability for endurance running (ER), defined as the ability to run long distances (>5km) using aerobic metabolism. Human ER capabilities derive from a suite of anatomical, physiological and behavioral features, many of which are uniquely evolved in humans, and which suggest that ER played an important role in human evolutionary history.

In order to consider the evolutionary origins of long distance running capabilities in humans, it is useful to begin with a review of ER ability in mammals in general, including other primates. Primates are not good runners, in part, because they have many specialisations (e.g. large hands and feet, relatively short forelimbs) that improve performance capabilities for climbing trees, but which hamper running performance. In addition, the forested environments in which most primates live do not afford much opportunity for running. Our closest ancestor,

the chimpanzee, is a typical example. Chimpanzees can sprint rapidly, but do so rarely and only for short distances (<100m).^[1] Thus, human ER abilities are unique among primates.

Human ER abilities are also unusual among mammals, even cursors (animals that have specialisations for running). Most mammals are good at sprinting, either because they are predators that rely on speed and agility or because, as prey, they need to escape their predators. Most mammals can out-sprint humans, who, as bipeds, lack the ability to gallop. Human running is mechanically most similar to quadrupedal trotting, which does not permit fast speeds.^[2] The maximum sprinting speed of humans is ≈ 10 m/s, which is above the maximum trotting speed of any non-human mammal, but well below the maximum galloping speed of other mammals of similar body mass.^[3] However, human ER speeds, which typically exceed 4 m/s and can reach 6.5 m/s in elite athletes, exceed the trot-gallop transition speed of all other mammals, regardless of size. This difference is significant because trotting is the quadrupedal endurance gait. Most quadrupedal cursors, such as dogs, can run long distances at a trot, but quickly overheat and fatigue when galloping, and can only do so for a long time in cool conditions that

lower the potential for hyperthermia. For example, a dog of similar body mass to a human (65kg) has a trot-gallop transition speed of 3.8 m/s and can sustain a gallop at 7.8 m/s in cool conditions for only 10–15 minutes.^[3] Horses with a maximum gallop speed of 8.9 m/s for 10km can easily outrun humans, but their sustainable galloping speed decreases considerably beyond 10–15 minutes. In repeated long distance runs, horses are constrained to a canter (a slow gallop) of 5.8 m/s for \approx 20 km/day.^[4] In short, for marathon-length distances, humans can outrun almost all other mammals and can sometimes outrun even horses, especially when it is hot.

The surprising ability of humans to run long distances so well, in terms of speed and distance, begs the questions of how, when and why these capabilities evolved. The easiest of these questions to answer is how, given the wealth of information available on the biomechanical and physiological demands of ER, which challenge the body in the following three major ways: (i) energetics; (ii) stabilisation; and (iii) thermoregulation. In terms of energetics, running uses a mass-spring gait with an aerial phase in which the body's center of mass (COM) initially falls during the first half of stance. As the COM falls, elastic energy is stored in the many tendons of the leg, which then recoil during the second half of the stance, pushing the body into another aerial phase. Importantly, the mass-spring gait differs fundamentally from the inverted-pendulum mechanics of walking and takes advantage of numerous tendons, such as the Achilles and the iliotibial tract, all of which are absent or tiny in other African apes.^[5] Humans also have spring-like ligaments in the feet.^[5]

Running also poses more challenges than walking for stabilisation, especially in inherently unstable, long-legged bipeds. Accordingly, humans have many derived features that help stabilise the COM of the trunk and head during running, most of which have little or no role during walking. These features include: (i) an enlarged *gluteus maximus*, which does not contract much during walking;^[6] (ii) a relatively narrow waist; (iii) a highly mobile thorax that is decoupled from the neck to permit counter rotation of the arms and trunk;^[7] and (iv) enlarged anterior and posterior semicircular canals that improve the sensitivity of the vestibulo-ocular reflexes

to rapid pitching movements generated in running but not walking.^[8]

Finally, the biggest physiological challenges that runners face are thermoregulatory, because the vastly greater rate and number of muscle cross-bridges needed to power running generates as much as ten times more heat than walking. Most mammals cease galloping after short distances because they cannot cool core body temperatures fast enough to avoid hyperthermia.^[9] Humans, uniquely, can run long distances in hot, arid conditions that cause hyperthermia in other mammals, largely because we have become specialised sweaters. By losing almost all our body fur and increasing the number and density of eccrine sweat glands, humans use evapotranspiration to dissipate heat rapidly, but at the expense of high water and salt demands.^[10] In contrast, other mammals cool the body by relying on panting, which interferes with respiration, especially during galloping which requires 1 : 1 coupling of breathing and locomotion.^[11]

The other questions that human ER capabilities pose are when and why did humans become good at running long distances? These questions are harder to answer, but the fossil evidence suggests that ER capabilities first evolved \approx 2 million years ago (Ma). Importantly, this transition, unique among primates, occurred long after the evolution of bipedal walking capabilities, which first emerged when hominids diverged from chimpanzees \approx 6Ma.^[12] Although there is debate, it is probable that early hominids, such as the australopithecines, combined habitual bipedal walking with some degree of tree climbing.^[5] However, features that would have improved ER capabilities, such as an expanded *gluteus maximus*, spring-like feet, more sensitive semicircular canals and so on, do not appear until the genus *Homo*, mostly in *H. erectus*.^[7] Because of gaps in the fossil record and because many soft tissues relevant to running do not fossilise, it is unclear whether *H. erectus* was as good at ER as later hominids such as archaic *Homo* and/or modern humans. Future research needs to address whether the transition to fully modern ER capabilities occurred before or after the origin of *H. erectus*.

As to why ER evolved, multiple lines of archaeological and recent ethnographic evidence suggest that ER was an integral part of making available to

early *Homo* a new ecological niche; that of a diurnal carnivore. In particular, small teeth, larger bodies and archaeological remains suggest that hominids started to incorporate meat and other animal tissues in the diet at least 2.5Ma, probably by hunting as well as scavenging. To be a carnivore, one must compete with other carnivores, yet these hominids were not only comparatively slow, but also lacked any weaponry more sophisticated and dangerous than simple stone tools and possibly sharpened, untyped spears.^[13] In this context, ER might have enabled hominids to scavenge carcasses from lions after they were abandoned but before hyenas arrived, as modern hunter-gatherers still do in East Africa.^[14] In addition, ER would have enabled hunter-gatherers in the hot, open habitats of Africa after 1.9Ma to hunt animals before the invention of better projectile weapons such as stone-tipped spears, which first emerged 200 000 years ago, and the bow and arrow, which was invented within the last 50 000 years.^[13] Before these inventions, hunters would have had to kill animals by spearing them at short range. Because one kick from a moderate-sized animal can be lethal, modern human hunters do not hunt with spears without first trapping or disabling an animal, using technologies not available for most of hominid evolutionary history. Yet, in hot weather, humans can effectively kill animals using persistence hunting, where a runner follows an animal, keeping it above its trot-gallop transition for several hours, driving the animal into hyperthermia so that it can be killed safely at close range. This kind of persistence hunting has been documented among many recent hunter-gatherer groups, including the Bushmen.^[15] Since ER is typically 30–40% more costly than the most efficient walking speed, the caloric costs of persistence hunting would have been minimal compared with the rewards of hunting a medium-to-large sized animal and would have put the hunter at minimal risk.

In short, the human ability to run long distances, such as a marathon, is neither a simple byproduct of the ability to walk bipedally, nor a biologically aberrant behaviour. Instead, running has deep evolutionary roots. Although humans no longer need to

run, the capacity and proclivity to run marathons is the modern manifestation of a uniquely human trait that help make humans the way we are.

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