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 \(\approx 10\) 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 sus-
tain 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 con-
siderably beyond 10–15 minutes. In repeated long
distance runs, horses are constrained to a canter (a
slow gallop) of 5.8 m/s for ≈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-pendu-
lum 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 liga-
ments in the feet.[5]

Running also poses more challenges than walk-
ning for stabilisation, especially in inherently unsta-
ble, 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 im-
prove 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 vast-
ly 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 evapo-
transpiration to dissipate heat rapidly, but at the
expense of high water and salt demands.[10] In con-
trast, 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 ≈2 million years ago (Ma).
Importantly, this transition, unique among primates,
ocurred long after the evolution of bipedal walking
capabilities, which first emerged when hominids
diverged from chimpanzees ≈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 climb-
ing.[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 rele-
vant 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 archaeo-
logical 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, untipped 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 moderately-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 hominin 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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