COMMENTARY

Marathon Running: The Macroevolution and Continued Adaptation of a "Uniquely Human Trait"

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According to the fossil record, endurance running capabilities first evolved roughly two million years ago: a divergent moment in human evolutionary history approximately four million years after the initial evolution of bipedal walking (Lieberman & Bramble, 2007). Fast forward to the present: in America alone, over 500,000 people complete at least one marathon in a given year (Humphrey, 2012). Because many people run ultra-marathons, races of distances that exceed 26.2 miles, and many runners never register for official races, the actual number of endurance runners in America likely exceeds one million people. Despite the fact that the majority of human beings find endurance running an abnormal and inexplicable behavior, it has only continued to rise in popularity across people of all ages and abilities since the initial "running boom" of the 1970s.

So, why do so many people participate in endurance/marathon running? Perhaps one reason is because we are one of the only species that can.

Most mammalian species can outsprint humans with ease because of their ability to gallop and our inability due to human bipedalism. However, regardless of their size, these mammals exhaust after covering distances of 10-15 km (Bramble & Lieberman, 2004; Lieberman & Bramble, 2007). Even specialized mammalian quadrupeds (e.g. canines, hyenas, horses, etc.) that can trot for relatively long distances begin to overheat and fatigue once a gallop pace is sustained for a reasonable amount of time, regardless of the temperature or environment. Elite racing horses, for example, can cover ~10 km before running speed declines (Minetti, 2003). Documented sporting events involving racing animals, such as horses or sled dogs, indicate that highly specialized quadrupeds are indeed capable of running over 100 km in a single day but only when a human driver forces them and most often in climates that are extremely cold to accommodate the animal's inability to thermoregulate as efficiently as a human being (Bramble & Lieberman, 2004; Lieberman, Bramble, Raichlen, & Shea, 2009), Combined with the artificial selection (i.e. breeding) that enhances performance in both dog and horse racing, these special conditions required for endurance running in other mammalian species highlight the unique, organic nature of human endurance running and make it all the more fascinating (Lieberman et al., 2009). According to the work of Lieberman and many others, humans can successfully engage in endurance running regardless of terrain, conditions, and environment because we are the only living species capable of handling both the biomechanical and physiological demands of a marathon, which include proper energetics, stabilization, and thermoregulation.

Certain physical features, altogether unique to humans, play an important role in endurance running. First and foremost, humans have large tendons and other anatomical features in their legs, which are absent in other primates, that store the elastic energy responsible for pushing forward during the second half of a runner's stance (i.e. Achilles, Iliotibial tract, etc.) (Lieberman & Bramble, 2007; Thorpe, Crompton, Gunther, Ker, & McNeill Alexander, 1999). The mass-spring mechanics that the Achilles tendon and the elastic longitudinal arch of the human foot make possible are particularly important as they conserve roughly 50% of the energetic cost of running with very little effect on the metabolic cost

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of walking (Ker, Bennett, Bibby, Kester, & Alexander, 1987). Similarly, a number of lower body muscles, including the gluteus maximus, are enlarged in humans. The gluteus maximus is one of the strongest muscles in the human body. Although it rarely contracts while walking, it plays an important, powerful role in the stabilization of human running (Aiello & Dean, 1990). Humans also have both a narrow waist (relative to the rest of the body) and a mobile thorax that functions independently of the neck. These elements of the upper body anatomy not only stabilize the center of mass of the trunk but also allow for full arm and trunk rotation (Aiello & Dean, 1990; Lieberman & Bramble, 2007). As bipedalism is inherently unstable at any speed, the free and opposing rotations of the trunk and the arms give human runners great stability against outside forces (Aiello & Dean, 1990; Hinrichs, 1990). Together, these features provide the balance, stabilization, and upper body relaxation required for marathon-distance running (Lieberman & Bramble, 2007).

Although these characteristics are all important for endurance running, the human method of thermoregulation likely plays the most important role in managing the physiologic demands of a marathon-distance run. Over evolutionary time, humans emerged with no fur and a large number of high-density eccrine sweat glands that in combination allow us to release heat from our bodies via evapotranspiration and high convection rates (Carrier, 1984; Lieberman & Bramble, 2007; Wheeler, 1991). In addition to the aforementioned features, humans also possess a long, narrow body shape relative to other mammals, allowing for dispersed heat dissipation across multiple body regions (Ruff, 1990). Overall, these thermoregulation mechanisms are efficient and far superior to those of most other mammals, including our primate ancestors, which often involve "panting" or nasal breathing (Lieberman & Bramble, 2007; Niinimaa, Cole, Mintz, & Shephard, 1981). These two processes are not only less efficient but also greatly interfere with essential components of any type of running: respiration and mouth breathing.

It is quite intriguing that humans are the only modern species capable of independent endurance running. However, the true physical beauty of the sport is that given appropriate time and proper training, almost any person who is capable of running has the potential to improve their endurance running abilities by far more than just a small margin. Both routine endurance running and marathon training, which involve runs of various times and distances over a three to four-month span, result in major physiologic adaptations that improve and prepare the body for future endurance endeavors. Taken together, the inherent evolutionary advantages and the capacity for extreme, non-evolutionary adaptations make humans the candidate species for endurance running.

Kevin and Keith Hanson, founders of the Hansons-Brooks Distance Project, owners of Hansons Running Shops, and creators of the Hansons Marathon Method, refer to the stress-adaptation phenomenon as the "Overload Principle": the idea that regular exposure to specific, targeted running exercise will enhance certain physiological functions and induce a training response. Over time, various small changes in the human body's biological functions result in rather large changes in muscle adaptation and both oxygen and energy utilization, ultimately leading to improved performance.

Routine endurance running stimulates positive adaptations in both the heart and circulation. Regarding the heart, endurance training yields increased coronary circulation, left ventricle thickening, ventricle chamber growth (i.e. endurance runners literally have bigger hearts, a non-pathologic condition known as exercise-induced cardiomegaly), and decreased heart rate (Humphrey, 2012). More blood is able to reach the heart, and more importantly, the heart is able to pump more oxygenated blood to the arteries with not only a much greater force but also a significantly reduced effort. Changes to the blood itself further enhance the impact of these cardiac adaptations. Studies have shown that total blood volume increases in endurance runners, typically resulting in a higher number of red blood cells in an increased, less viscous total volume (Humphrey, 2012). As a result of these changes and the increased capillary

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density that occurs in the leg muscles, more oxygenated blood reaches the exercising muscles in an improved, more efficient exchange (Humphrey, 2012).

In addition to increased capillary density, many important adaptations occur in the skeletal muscles as a result of endurance training, including mitochondrial growth, increased mitochondrial density, and improved mitochondrial enzyme levels and function (Humphrey, 2012). Since mitochondria are the "cell's powerhouse," utilizing fatty acids, amino acids, and carbohydrates to produce energy, these improvements give endurance runners "more bang for their buck" – producing more energy at the same rate and maximizing fatty acid utilization all while conserving the body's precious glycogen stores (Humphrey, 2012).

With the aforementioned sub-cellular adaptations, routine endurance running also alters both slow- and fast-twitch muscle fibers (Humphrey, 2012). Despite their name, slow-twitch fibers play a key role in endurance running due to both their high fuel efficiency, resulting from high capillary density, high mitochondria density, and high oxidative capacity, as well as their extreme fatigue resistance. A runner's basal level of slow-twitch fibers is genetically determined. However, endurance training fosters the development of the fatigue-resistant slow-twitch fibers as well as type I fast-twitch fibers, which play a key role in endurance running once the slow twitch fibers have been exhausted (Humphrey, 2012). In comparison to other fast-twitch fibers, type I fibers not only have a higher fatigue resistance but also have higher mitochondria density, capillary density, and oxidative capacity. These specific muscle fiber adaptations can occur in as little as 10 weeks of routine running, yielding improved endurance/performance and preventing a runner's legs from hitting the previously unavoidable "wall" (Humphrey, 2012).

In the field of endurance running, an individual's anaerobic threshold – the moment when aerobic pathways provide some energy for muscle contraction but are no longer fast enough to provide all of the energy required for the exercise – is often the best predictor of endurance performance. Taken together, all of the aforementioned adaptations improve performance by increasing a runner's anaerobic threshold. Through high-volume, continued aerobic training, endurance improves, resulting in reduced reliance on less efficient anaerobic metabolic pathways. By increasing the anaerobic threshold, endurance runners are better equipped to utilize fatty acids as energy, an oxygen-dependent process, ultimately preserving carbohydrate stores and preventing the body from reaching a point of total exhaustion.

But why did humans start running in the first place?

Lieberman et al. loosely hypothesize that endurance running evolved as a necessary method of hunting, as hominids and early *Homo* species had to run down and track their 'moving food' over long distances, as they lacked the tools (tipped spears, bow and arrow) required to efficiently kill from afar. As their mammalian prey fatigued, our evolutionary ancestors needed to maintain enough energy to closely approach their prey for the kill. Research from other groups indicates that these persistence hunting methods would impose massive energy costs on the hunters (Steudel-Numbers & Wall-Scheffler, 2009). However, evidence from modern hunter-gatherer studies suggests that the net energy gained from a successful hunt would indeed make the theory plausible (Liebenberg, 2006). If this hypothesis held and "endurance hunting" was truly a means of survival, *I wonder how many pre-human Homo species would qualify for Boston?*

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