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Born to Run

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The proposed adaptive benefits of human bipedalism are well known by now. They all focus on making walking in open spaces more efficient and safe and, in the fossil record, are thought to mark the beginning of the hominins, going back through the australopithecines to the very earliest members of our lineage. In this selection, however, Adam Summers reports on new research that indicates bipedalism may also have evolved to benefit endurance running and that the *kind* of bipedalism we modern humans have is not shared by our earlier ancestors. Indeed, the australopithecines are more apelike in some of their features related to locomotion. This seems to make members of genus *Homo* even more distinct from the increasingly large array of possible early hominins.

As you read, consider the following questions:

1. What is endurance running and how does it differ from sprinting? What other animals are good endurance runners?
2. What is the physical evidence for our endurance running ability? How do our traits in this regard differ from those of apes and early hominins?
3. What might have been the benefit of endurance running to early members of genus *Homo*?

Paleoanthropologists, the paleontologists of the human lineage, have a tough task. Hominid fossils are scarce, and they're usually incomplete. Worse, the missing bits are often the ones investigators would most like to find—making it difficult to assemble an evolutionary tree of fossil hominids.

But if that's a tough job, imagine what life is like for anyone seeking to describe how bones and muscles functioned in ancient hominids. The scarcity and incompleteness of hominid fossils has often prolonged biomechanical debates concerning hominids. "Lucy" *(Australopithecus afarensis)* is a case in point. She was discovered more than thirty years ago, but a disagreement about whether those of her species walked more like a person or more like a chimpanzee was only recently decided in favor of the former.

That debate was important because a long-standing hypothesis holds that long-distance walking migrations played an important role in the evolution of our genus *Homo*. Many of the features that distinguish the various species of *Homo*, which lived in the open savanna, from Lucy and her kin, which were forest primates, are traits useful for walking: longer legs, narrower waists, shorter toes. Now Dennis M. Bramble, a biomechanist and vertebrate biologist at the University of Utah in Salt Lake City, and Daniel E. Lieberman, a biomechanist and anthropologist at Harvard University, have added a major new wrinkle to the story of human bipedalism. The two argue, in a review synthesizing several decades' worth of work by a large number of investigators, that running also played an important role in shaping our species.

If you've ever chased a cat that's trying to avoid a bath, you have every right to conclude that, for our size, we humans are pretty poor runners. But chasing a cat is sprinting. Where we excel is endurance running. Moreover, we run long distances at fast speeds: many joggers do a mile in seven-and-a-half minutes, and top male marathoners can string five-minute miles together for more than two hours. A quadruped of similar weight, about 150 pounds, prefers to run a mile at a trot, which takes nine-and-a-half minutes, and would have to break into a gallop to keep pace with a good recreational jogger. That same recreational jogger could keep up with the preferred trotting speed of a thousand-pound horse.

Good endurance runners are rare among animals. Although humans share the ability with some other groups, such as wolves and dogs, hyenas, wildebeest, and horses, we alone among primates can run long distances with ease.

But what evidence can support the idea that endurance running by itself gave early humans an evolutionary advantage, and that it wasn't just "piggybacking" on our ability to walk? Many traits, after all, are useful for both activities; long legs, for instance, and the long stride they enable, are helpful to walking as well as to running. But running and walking are mechanically different gaits. A walking person, aided by gravity, acts as an inverted pendulum: the hip swings over the planted foot [*see "The Biomechanist Went Over the Mountain," by Adam Summers, November 2004*]. In contrast, a runner bounces along, aided by tendons and ligaments that act as springs, which alternately store and release energy.

Bramble and Lieberman point to a number of features, preserved in fossils, that imply *Homo* adapted to a bouncy gait—whereas *Australopithecus* stuck with walking. . . . Fossils lack tendons and ligaments, of course, but traces of their attachment points are sometimes present, and the characteristics of the missing tissue can be inferred by comparing how the attachments fitted with the rest of the animal's anatomy. For example, the Achilles tendon, attached to the heel bone, is one of the most important elements in a human's bouncy gait. In *Australopithecus*, however, the attachment point of the tendon is distinctly chimpanzee-like. Another spring occurs in the foot itself: tendons in the sole of a human's foot keep it arched. The arch flattens and springs back with each step. In contrast, Lucy had only a partial arch. *Homo habilis* had a full arch. Chimpanzees have no arch at all.

In addition to springs, endurance running requires more stabilization of the trunk than walking does. Members of the genus *Homo* have substantial gluteus maximus (butt) muscles. Those muscles have numerous large attachments from the hip to the base of the spine. In *Australopithecus* fossils, though, the muscle has a much more limited area of attachment. If you've seen a chimpanzee in trousers, you know how baggy they look. Chimpanzees are gluteally challenged as well. Large butt muscles are not only better looking in pants; they also make for efficient energy transfer during running by stabilizing each hip. But the muscles are not used for walking on level ground.

In contrast with the trunk, the shoulder of the chimpanzee is well stabilized, tied to the spine and the head by several strong muscles. Lucy retained the stabilized shoulder, but in humans those muscle connections are less robust—and for good reasons. When we walk, our shoulders don't move much, but when we run, because of the relatively loose attachment, the shoulders rotate strongly one way while the hips rotate the other. The counterrotations help keep us in balance. And because only one part of the trapezius muscle attaches to the head, we can swing the upper body without inadvertently rotating the head—which enables us to see where we're going.

In spite of the loose attachment between head and shoulders, running joggles the head more than walking does. *Homo* therefore has several "antibobblehead" adaptations that other apes and *Australopithecus* lack. The first is a modification of the semicircular canals, the organs in each inner ear that tell the brain which way is up. Three such canals sit at right angles to one another in each inner ear. Two are enlarged in *Homo*, and the size makes it easier to sense, and presumably to counteract, a nodding head. An elastic ligament that runs from a ridge at the base of the skull to the base of the neck, damps the bobbing effect. Analogous ridge structures, to which damping ligaments can be attached, occur in dogs and horses, the other long distance runners, but not in Lucy.

Bramble and Lieberman's wide-ranging analysis makes important corrections to the scientific picture of early humans. Our ancestors may have ranged across large distances in the heat of the African savanna in relatively short spurts of long-distance running, as well as by walking. They may have been trying to maximize the chance of encountering carrion before other scavengers did, or perhaps they were adapted to running down prey before spear throwers or bows were invented.

In any case, our current appetite for jogging is made possible by the early selective pressures that made humans one of the most accomplished endurance-running animals. For myself, though, I imagine another adaptation. The heat and the running must have been powerful motivators for our ancestors to sit in the shade and ponder how to affix a rock to a stick.

Note: There is a new idea that "arboreal bipedalism" might have been a precursor to our bipedalism. Some apes, especially orangutans, move along branches too flexible to support their weight by standing on the branch and supporting themselves further with hands extended to a branch above. See, for example, O'Higgins, P. and S. Elton. Walking on trees. *Science* 316:1292–94, and the cover image of my *Biological Anthropology*, 6th ed. (2010, McGraw-Hill).