Biomechanical research reveals a surprising key to the survival of our species: Humans are built to outrun nearly every other animal on the planet over long distances.

by Ingfei Chen

Late one night over beers in the Welsh hamlet of Llanwrtyd Wells, an innkeeper got into an argument with a foxhunter about who could run faster, man or horse. The innkeeper insisted that over many miles, a human runner would have greater stamina, and prevail. Thus was born a tradition: Every year since 1980, Llanwrtyd Wells has hosted the Man Versus Horse Marathon, which pits hundreds of runners against dozens of horses with riders. On two legs or four, contestants take on 22 miles of challenging trails laced across a dazzling green countryside. They trot through fragrant pine forests, scramble up mountainous rock-strewn sheep trails, cross rolling moorlands, and ford rivers. In June 2004, for the first time ever, the human won. The innkeeper was delighted—and so were University of Utah biologist Dennis Bramble and Harvard University paleoanthropologist Daniel Lieberman. That summer the two scientists were putting the finishing touches on a theory with a new view on how conditions millions of years ago molded the way humans move today. The standard explanation among physical anthropologists has long been that early hominids left life in the trees to forage on the open savanna and that walking upright was the key to surviving in that new environment. Bramble and Lieberman do not dispute this general theory, but they have identified a suite of traits in the human anatomy that add a dramatic twist to the story line.

The traits appear to be specifically adapted for running—and for jogging for long distances. So Bramble and Lieberman were not at all surprised that a man won the Man Versus Horse Marathon. It fits their hypothesis. Unlike many mammals, not to mention primates, people are astonishingly successful endurance runners, "and I don't think it's just a fluke," Lieberman says. He and Bramble argue that not only can humans outlast horses, but over long distances and under the right conditions, they can also outrun just about any other animal on the planet—including dogs, wolves, hyenas, and antelope, the other great endurance runners. From our abundant sweat glands to our Achilles tendons, from our big knee joints to our muscular glutei maximi, human bodies are beautifully tuned running machines. "We're loaded top to bottom with all these features, many of which don't have any role in walking," Lieberman says. Our anatomy suggests that running down prey was once a way of life that ensured hominid survival millions of years ago on the African savanna.

Although Bramble has studied locomotion in animals ranging from tortoises to jackrabbits for 40 years, he was first tipped off to the hypothesis that humans were born to run by one of his students, David Carrier. In the 1970s, Carrier was assisting with Bramble's studies of how dogs, horses, and people regulate breathing while running. A marathoner himself, Carrier began to wonder about the role of endurance running in human evolution. People, he noted, can shed heat quickly—not by panting, like most animals, but by perspiring through millions of sweat glands. A lack of fur also helps dissipate heat more quickly.

Other researchers have proposed that such features emerged because our ancestors had to cope with the sun as they moved from a shady forest habitat to the scorching savanna. Carrier suspected that these traits were more relevant for handling physical exertion. The human body generates six times more heat when sprinting at top speed than when sitting in the sun. Most animals, humans included, must stop trotting when they overheat, or they die.

(In one legendary experiment, Harvard biologists stuck a rectal thermometer into a cheetah, put the cat on a treadmill, and found that it refused to move once its temperature hit 105 degrees Fahrenheit, even though it was loping well below its top speed.) Controlling body temperature, Carrier once wrote, "is critical for animals that run for extended periods." Given that humans excel at releasing heat and distance running, he speculated that we were built to run far and wide.

"I didn't buy it at all," Bramble says. Like most of his peers, Bramble's first reaction to Carrier's hypothesis was that "humans are pitifully slow." From the perspective of a vertebrate morphologist, humans lack one of the most obvious features of animals adapted for serious speed: a tail. In creatures that cover ground bipedally, such as kangaroos, kangaroo rats, and roadrunners, "the tail is the major balance organ," Bramble says. "In the whole history of vertebrates on Earth—the whole history—humans are the only striding biped that's a runner that's tailless."
Still, Bramble eventually came to realize that people turn in remarkable performances. He once filmed a horse cantering, with Carrier running alongside at the same pace. The movie showed that Carrier’s legs were churning more slowly than the horse’s, which meant that the student’s strides had to be spanning more distance per step than the horse’s.

Although Carrier moved on to other research, Bramble grew convinced that his student had discovered something. During a visit to Harvard in 1991, Bramble encountered Daniel Lieberman, then an anthropology Ph.D. student, making a pig trot on a treadmill. To glean insights into how bones grow—and thus to better interpret fossilized human jaws and skulls—the student wanted to see whether the repeated impact of running would spur a thickening of the pig’s skull. “You know,” Bramble said, “that pig’s not holding its head still.” He went on to explain that adept runners like horses, dogs, and rabbits keep their noggins remarkably steady as they lope, thanks to an obscure bit of anatomy called the nuchal ligament. It’s a tendonlike band that links the head to the spine. People, he said, have a version of this band.

Rummaging through a collection of replicas of fossilized primate bones in a nearby lab, Bramble pointed out that the nuchal ligament leaves a trace—a delicate ridge—where it attaches at the base of the human skull. Then the scientists noticed the ridge in a pitted, yellowed skull of our 2-million-year-old relative Homo erectus—but not in older hominids known as australopithecines, who walked the earth as far back as 4.4 million years ago. “Holy moley!” Lieberman thought. “There’s something going on here, and what’s more, we might be able to study it in the fossil record.”

"Once the idea is in your head, then you start thinking about things differently," Lieberman says. A short 41-year-old with a receding hairline, a slight paunch, and disarming dimples, Lieberman doesn't look athletic, but he has been a jogger since his teens. I joined him for his morning run with his dog, Vashli, a border collie mix, whom he easily proved he could outlast. Lieberman says it's wrong to assume, as many do, that running is like walking. The two motions are strikingly different. He demonstrates that during walking his heel hits the ground first, the leg straightens, and then the body vaults over it.

"Your center of gravity, which is basically near your belt buckle, r-i-i-i-ses"—he takes a slow-motion step forward with his right leg and pauses, now up on the ball of his right foot—"so that it's over your leg." The body has now stored potential energy. The arch of the foot stiffens, and Lieberman pushes off against it. As he tips forward, potential energy converts to kinetic energy, and he swings his left foot ahead to complete the stride.

But in running, he says, the legs become springs. You land on and squash the entire arch and bend your knee. So initially the body’s center of gravity falls. "You go down—and then you go up," Lieberman says. Kinetic energy from the crash landing is stored in the many stretchy tendons of the arch and the leg, most notably the huge Achilles tendon connecting calf muscles to the heel bone. Like rubber bands, the tendons extend and then recoil—boing!—to launch you onto the next step.

"So why do we have all these tendons in our legs?" Lieberman asks. "You don't evolve big tendons unless you're a runner." Kangaroos, antelope, and other serious animal runners all have a great set of springs, which do nothing for walking. So our tendons can’t be explained as being necessary for walking.

Part by part, Bramble and Lieberman have reinterpreted the hominid physique by juxtaposing bits of fossil evidence with what's known about the physiology and biomechanics of jogging. Although much of the anatomy that lets us lope is the same equipment that humans first evolved for walking, the researchers say many of our physical traits seem tailor-made for sustained running.

To test their ideas, they conduct biomechanical studies in Lieberman’s lab—Room 53 in Harvard’s small redbrick Peabody Museum. The space looks more like a meld between a sports medicine clinic and an untidy engineering workshop than an anthropologist's sanctum of precious old bones. In addition to a gray-and-black running treadmill, there are wall shelves and counters cluttered with boxes of cotton applicators and latex gloves, containers of antiseptic, a small toolbox, tangles of electric cords, and plastic models of human parts, including a gigantic ear.

In one recent experiment, a volunteer named Jeff, dressed only in dark Lycra shorts and white socks, looked like a guinea pig trapped in a bad sci-fi flick. To track the electrical activity of key muscles, Lieberman and a postdoc, David Raichlen, had tapped circular force-detecting pads to the bottoms of Jeff’s feet and carefully rigged other parts of him with electrodes. Wires from those sensors ran through a small preamplifier box strapped to his lower back and then to a nearby computer.

To capture an image of his movement, they attached little silvery gray reflective balls onto Jeff's shoulders, hips, knees, and other joints. Three infrared cameras would track the balls' motion and record a stick-figure animation of him as he moved. Finally, to measure forces acting on his skull, the researchers mounted an inch-long accelerometer and gyroscope onto a small round tin and tied it all on top of Jeff's head with a black mesh do-rag that knotted securely under his chin.
Then Lieberman and Raichlen put Jeff on the treadmill and started it up. "Focus on the gazelle on the savanna," Lieberman instructed over the hum of the machine, indicating a big black X on a sheet of paper taped to a shelf straight ahead. The researchers gradually cranked up the pace until Jeff was pounding along at a hard run, sweaty and breathless. "Your gluteus is getting a serious workout," Lieberman said cheerfully.

The goal of the exercise was to understand how joggers stabilize their heads and torsos—part of the distinctive human balancing act that puzzled Bramble years ago. Without the balancing help of a tail, how do we avoid falling over when we run? The butt, it turns out, is crucial—right up there with the chin among traits that make us uniquely human. Chimps and other primates have little buns. Our own rear ends are huge; the upper part of the gluteus maximus is greatly expanded. Although few scholars have studied its role in running, the butt is, according to Bramble, "basically a substitute for a tail."

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The treadmill studies support that idea. A few months later, Lieberman showed the results from Jeff and 15 other joggers, partly summarized in a conference presentation ("Why Is Our Gluteus So Maximus?"). Sitting at his computer in shorts and flip-flops, Raichlen pulled up Jeff's data: a rainbow-colored series of 16 synchronized electrical recordings from all the sensors. Looking like an EKG signal, the electromyograph, or EMG, reading from the gluteus maximus, in red, showed little activity when Jeff strolled. But once he broke into a jog, boom!—the red line tightly zigzagged. The faster the pace, the bigger the spikes, like an earthquake signal on a seismograph.

What that shows, says Lieberman, is that the butt isn't much involved during walking. In running, however, the body leans forward so that each time the leading foot strikes the ground, the trunk wants to topple forward. The gluteus maximus prevents that: It fires just before the foot slams into the floor, creating a braking action that keeps the torso from falling down.

Meanwhile, the way we pump our arms back and forth in a trot helps steady us too. And based on their experiments, the researchers suspect that the motions of our shoulders and arms actually help counterbalance the head, preventing it from pitching forward on each landing. Simultaneously, with each heel strike, certain shoulder muscles contract and put tension on the nuchal ligament, pulling up the skull and keeping it level.

Our long neck is also important for running, Bramble says, because it allows the shoulders to twist freely of the head as we gaze forward. Chimps, in contrast, have hulking muscles anchoring the skull to the shoulders, which appear permanently shrugged—an orientation ideal for reaching overhead to dangle from tree branches. Controversial fossil evidence hints that australopithecines also had chimplike shoulders. But by the time of 2-million-year-old Homo erectus, says Bramble, hominids had lowered their shoulders, losing the thick, muscular connections to the head.

These running features, the researchers argue, are unmistakably obvious once you look for them. What's really hard to pin down, they admit, is when these adaptations emerged. How do you figure out when the first human butt appeared on the savanna? Muscles, tendons, and sweat glands don't fossilize, and old bones can't reveal precisely how their owners moved. Still, between biomechanical studies and bone analyses, it's possible for researchers to infer whether a fossil hominid was a jogger.

For example, most scientists reasoned that the 3.2-million-year-old hominid Lucy, with her chimplike build, couldn't have been a good endurance runner. She was squat, with short legs, a wide waist, long arms, and long, curving fingers and toes that suggest a tree-climbing lifestyle. Although researchers disagree on Lucy's gait while walking upright, nobody thinks she could have strolled like a human. Yet more than a million years later, Homo erectus roamed Africa with a much longer, leggier build, sporting a dramatically different set of physical changes that made it harder to climb trees but easier to jog, Bramble says. "All the running equipment's already there."

What biomechanics and paleontology studies cannot reveal is why these transitional hominid types forsook life among the boughs to become earthbound marathon runners. Archaeological studies at hominid sites offer one strong clue—animal bones. About 2.6 million years ago, our forebears started eating meat and marrow, rich sources of protein and fat that perhaps eventually fueled the growth of larger brains. Bramble and Lieberman find it conceivable that endurance running helped hunters pursue prey to exhaustion.

Back in the 1980s, Carrier had read ethnographers' accounts of indigenous peoples who chased deer, antelope, and kangaroos to exhaustion under the scorching sun. The Tarahumara of the mountainous desert of northwestern Mexico, for example, were legendary runners. But by modern times, their running tradition had turned to sport: Men wearing simple tire-tread sandals bound with leather thongs compete in a 24-hour footrace that involves kicking a ball over about 100
Miles of mountainous road. So Carrier, a triathlete in college, took it upon himself to prove his case. He and his younger brother, Scott, went to the desert in Utah and Wyoming to chase pronghorn antelope. The beasts ditched them every time. The sleek, bouncy animals would join up with others, and soon the men would be huffing after a dozen of them. "You wouldn't know which were the animals you started with," Carrier says.

For direct evidence of endurance hunting, Bramble and Lieberman point to the observations of Louis Liebenberg, author of The Art of Tracking: The Origin of Science, who has spent time on the traditional hunts of the Bushmen hunter-gatherers in the central Kalahari Desert in Botswana. Liebenberg ran with them when they chased down kudu antelope on two occasions. For eight other hunts he trailed them in his Land Cruiser, sometimes with a GPS device. The men attempted to run prey to exhaustion only when temperatures neared 100 degrees F, says Liebenberg. Three men would gulp a lot of water and head out together. Two initially did the hard work of tracking and pursuing over the arid grassland and woodland terrain, while the other held back. Eventually, the leaders dropped behind, leaving the third man to hound and spear the antelope when it reached its limit. "The animal will either just completely collapse, or it will actually slow down to a point where it just stands there . . . with sort of glazed-over eyes," Liebenberg says. "Essentially, you're pushing the animal to overheat." The hunters would then walk home with the meat, enough to share—in small portions—with the tribe.

During a chase, Liebenberg noted that the men maintained speeds of around 4 to 6 miles per hour, for anywhere from two to six and a half hours, and traversed up to 22 miles of terrain. These stats fall well within the performance range of the world's fastest competitive marathoners, who set a pace of roughly 12 miles an hour to cover 26 miles, albeit under far less harsh conditions.

Although Liebenberg's observations support the runner-as-hunter hypothesis, Bramble and Lieberman think early Homo would more likely have first run to scavenge prey killed by other carnivores—a strategy the Hadza people of East Africa are known to use. When leopards or hyenas bring an animal down, the hunters "can spot these fresh kills at a distance from the vultures circling above," Bramble says. A carcass is an ephemeral treasure, picked clean within hours, so the Hadza quickly head off running, chase away the carnivores, and take what's left.

Of course, no one knows whether scavenging reaped enough caloric and nutritional returns to make it worthwhile for our forebears. But Bramble and Lieberman feel that the collective evidence, fielded from so many different angles, makes a compelling case for the running hypothesis. Even ordinary studies of human physiology, for example, suggest that humans are so adapted for intense physical activity that a sedentary lifestyle spawns modern-day scourges like diabetes and heart disease. Additional support could come from the chimpanzee genome, which may allow researchers to clock when the genes for slow-twitch muscle fibers—crucial for running long distances and plentiful in people but not chimps—diverged in the common evolutionary history of humans and apes. Other clues could come from tracing the genes involved in our abundant sweat glands and loss of body hair.

Meanwhile, other researchers are looking for holes in the argument. Functional morphologist Brigitte Demes, at the State University of New York at Stony Brook, notes that the gluteus maximus is absolutely essential for rising from a squatting posture at rest or during foraging, so it might not have evolved just for running. Stony Brook anatomist Jack Stern, famed for analyses of how Lucy walked, says it's a tough call to classify the Achilles tendon as an adaptation for jogging. Longer legs evolved in many animals through the extension of lightweight tendons rather than heavier muscle, thus producing a limb that took less effort to swing—a change that would save energy during walking, Stern says.

Nonetheless, Stern credits Bramble and Lieberman for a clever, coherent theory. "In essence, this is what Darwin did when he wrote On the Origin of Species: He took a series of facts and wove a beautiful, elegant story," Stern says. His own hunch is that the running hypothesis is correct, but it will take decades of scientific squabbling to confirm it. "This is just the beginning," he says. And even Demes, although skeptical of the running hypothesis, can't think of an alternative explanation. "That might actually be their strongest argument," she admits. "Why do we have this skill to go long distances for extended periods of time? Because you really don't see that in other primates." Bramble and Lieberman have received a flood of enthusiastic e-mail messages (and even poems) about their work, mostly from runners. "Sometimes you come across an idea that for some reason has been kind of overlooked. But it's just obvious. And those are the ideas, I think, that touch a nerve," Lieberman says. The evolution of walking was unquestionably fundamental to becoming human, he says, but running played a pivotal role too. "If we can get people to agree on that, I'll go to bed happy."