PHYSIOLOGY

A New View of How Leg Muscles Operate on the Run

You probably think of the muscles in your legs as motors, contracting and relaxing to drive legs up, forward, and down when you run. But new results reported on page 1113 by comparative physiologist Thomas Roberts of Northeastern University in Boston and his colleagues suggest that what actually propels you is a set of springs, consisting mainly of the tendons that attach the muscles to the bones. Often, the role of the muscles, they found, is to hold the ends of these springs rigid so that they can store energy as you land after each step.

The findings, from an experiment in which the researchers directly monitored a leg muscle in turkeys as they ran on a treadmill, apply only to running on level ground. But they challenge the long-standing assumption that muscles always do actual work, shortening against resistance, to propel an animal forward—a view based on studies of isolated muscles or analyses of high-speed films of animals in motion. Instead, sensors implanted in the turkey leg showed that the muscle shortens slightly before the foot is planted and then simply exerts the force needed to keep the tendon stretched while the foot is on the ground, storing energy for the next stride. "The muscle is not doing any work," says physiologist Robert Full from the University of California, Berkeley.

That finding helps explain an observation that has long puzzled muscle physiologists: Larger animals expend less energy per pound to propel themselves forward than small animals do. Physiologists tended to assume that the muscles and tendons in the larger animals simply use energy more economically as they do work. But the turkey studies indicate that the amount of work done has little to do with this difference.

Instead, the answer lies in the fact that muscles that develop force more slowly require less energy, notes Peter Weyand, who did this work with Roberts at the Harvard lab of the late Richard Taylor: Larger animals take bigger steps and their feet stay on the ground longer, buying their leg muscles extra time to generate the necessary force on their tendons.

For the current experiments, Roberts worked with turkeys because their tendons are better suited than other animals' to the technique he and his colleagues used for measuring the force generated by muscle contraction. To do this, they glued tiny strain gauges, which are commonly used to detect bending in bone or stressed steel, to each side of the tendon attaching the animals' gastrocnemius muscles (the equivalent of the human calf muscle) to the heel. The tendons of most animals are so elastic that the gauges would "pop right off" when a muscle pulled on them, says Roberts. But in the turkey, a large part of the gastrocnemius tendon is calcified and stiff. Consequently, the gauges stay mounted and can measure the stress exerted as the muscle contracts.

At the same time that the researchers were measuring force, they also wanted to see how much the muscle was contracting as the turkeys ran. For this measurement, Richard Marsh from Northeastern sewed two piezoelectric crystals, one about 2 centimeters higher than the other, onto the gastrocnemius muscle. When the investigators sent a small electric current into one crystal to make it vibrate, the other crystal sensed the vibrations after a lag that depended on the distance separating the two. How much the muscle shortened as it contracted could then be determined from changes in the travel time.

TOM ROBERTS

Turkey trot. Monitoring the leg muscle reveals how turkeys—and perhaps other animals—run.

The results of these measurements were surprising. For one, the researchers observed that the relaxed muscle itself acts as a spring at times, lengthening as the leg swings forward, then recoiling as the foot heads toward the ground. While the turkey's foot is on the ground, the muscle generates force but shortens by just about 7% of its length. This small change translates into very little work output. Instead, "the force the muscles are generating in the stance phase were largely isometric," comments biomechanicist Andrew Biewener of the University of Chicago. "They are simply acting as force generators."

And the strain gauges indicated that muscle exerts strong tension—100 newtons—on the tendon, particularly as the turkey plants its foot. The force exerted by the muscle enables the tendon and the sheath covering the muscle to stretch and store gravitational energy, just as a pogo stick stores energy each time its rider lands. The release of that energy is what propels the bird forward, Roberts says. "Most of the work is done passively in the elasticity [of the muscle and tendon]," Biewener adds.

"At first glance, that's counterintuitive," notes Thomas Daniel, a biomechanicist at the University of Washington, Seattle, because it implies that a running animal can get by on gravitational energy alone, without any additional energy input—as if a ball could bounce indefinitely. In fact, as Biewener points out, once a turkey or other running animal is in motion, it doesn't need to do much work to keep itself going. The small amount of shortening Roberts and his colleagues measured while the foot is planted is apparently enough to make up for friction and other inefficiencies.

The situation changed, however, when the turkeys ran on an inclined treadmill. Their gastrocnemius muscles shortened more, working harder than they did on level ground. In addition, to produce the same force as it did on level ground, the amount of muscle used had to triple. "A lot more muscle is having to get recruited to get more force when the animal is [moving] uphill," notes R. McNeill Alexander, a biomechanics specialist at the University of Leeds in the United Kingdom.

Not everyone is certain that Roberts's experiments will be the last word in muscle function. Muscle physiologist Robert Gregor from the Georgia Institute of Technology worries that the piezoelectric crystals may not reliably estimate length changes. The speed at which the signal travels from one crystal to another may vary, depending on the properties of the tissue between the two crystals, he notes.

Roberts, however, thinks the variability in signal travel time is too small to be a major concern, although he agrees that studies need to be done in other muscles to see if they work the same way. But to many biomechanics researchers, the familiar machinery of running already has a whole new look. Comments Daniel: "It uses an ingenious set of experimental methods, and the results are incontrovertible."

–Elizabeth Pennisi