Muscular Force in Running Turkeys: The Economy of Minimizing Work

Thomas J. Roberts, *et al.*

TATCATCATGGA-3′; 1341, 5′-GCCCTGTGAGT-GAAGAAAGGC-3′; and 1550, 5′-GCAAATGAGTA-GATGTCTGCT-3′. We followed the procedure in (7), except that the primer annealing temperature was 58°C, and second-round amplification was performed with both primers at 0.1 μM. The primer numbering refers to the position of the 3′ base in the published chicken c-mos sequence (12). We sequenced products using the Taq DyeDeoxy Terminator Cycle Sequencing kit (Applied Biosystems) and analyzed them on an Applied Biosystems 373A DNA sequencer. The sequences were aligned with the human, mouse, Xenopus, and chicken c-mos sequences (12), and 599 homologous positions were identified (positions 186 through 788 of the chicken sequence). The effective sequence length was estimated to be 250 from the number of leucine and third codon positions and variation observed in the 10 avian orders.

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11. Sequences are available from GenBank, accession numbers U88000–88028 (for 12S sequences) and U88417–88430 (for c-mos sequences), and both aligned data sets are available on World Wide Web site http://www.massey.ac.nz/~wwplbio/research/farside/programs.htm

12. When the phylogenetic relation of a taxon is uncertain (for example, tropicbird), we formed pairs of taxa using the closest genetic outgroup found within the data set (gull, in this case). The pairs used were: rhea versus tinamou, moa, ostrich, emu, cassowary, kiwi; ostrich versus emu, cassowary, kiwi; cracid versus guinea fowl, chicken; chicken versus guinea fowl; penguin versus albatross; loon versus shearwater; and gull versus tropicbird.

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Muscular Force in Running Turkeys: The Economy of Minimizing Work

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During running, muscles and tendons must absorb and release mechanical work to maintain the cyclic movements of the body and limbs, while also providing enough force to support the weight of the body. Direct measurements of force and fiber length in the lateral gastrocnemius muscle of running turkeys revealed that the stretch and recoil of tendon and muscle springs supply mechanical work while active muscle fibers produce high forces. During level running, the active muscle shortens little and performs little work but provides the force necessary to support body weight economically. Running economy is improved by muscles that act as active struts rather than working machines.

Running is a bouncing gait in which mechanical energy is absorbed to slow and lower the body in the first half of a step and released to lift and accelerate the body in the second half of a step. Although some of this work can be provided passively by elastic energy storage in tendons (1, 2), active muscles must provide the force necessary to support the body and maintain tension on tendon springs. Differences in the energy cost of running across animal size and speed are proportional to the

cost of producing this force (3) but not to the rate at which mechanical work is performed (2). In vitro, muscles that contract isometrically (without shortening) perform no work but use metabolic energy and produce high forces. In contrast, a shortening contraction that maximizes mechanical work rate (power) produces only one-third the force of an isometric contraction, due to the characteristic force-velocity relation of skeletal muscle (4). This trade-off between work rate and force output suggests that animals could minimize the cost of producing force during running by operating active muscle fibers isometrically while the stretch and recoil of tendon springs provide the work of the bouncing body.

We used surgically implanted sonomicrometer crystals to measure fiber length and strain gauges to measure muscle force in the

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lateral gastrocnemius muscle of running turkeys (Fig. 1) (5). These methods avoid the uncertainties associated with the determination of muscle length from film measurements (6) and can discriminate between length changes in muscle fibers as opposed to those of passive tendons. Sonomicrometry has been used successfully to measure skeletal muscle length changes in situ and during walking in cats (7, 8), and force buckles have provided measurements of forces in individual muscles (9). Direct measurements of muscle work require simultaneous determinations of both muscle force and fiber length.

During level running, large changes in muscle length occurred only during the swing phase when the foot was off the ground (Fig. 2). The force produced during the swing phase

acts to decelerate the foot (tarsometatarsus and phalanges) during ankle flexion and then accelerate the foot toward the ground as the ankle extends. Surprisingly, much of this force was produced passively by the springlike behavior of the muscle as it is was stretched beyond its resting length. We confirmed that much of this force was produced passively by observing that stretching the muscle to the same lengths in an anesthetized bird (with no muscle activity) produced forces similar to those observed during the swing phase of running. Some active muscle force production also occurred during the swing phase. However, the amount of muscle activity during the swing phase was small; much of the force during each stride was developed before any electromyogram (EMG) activity (Fig. 2), and

the total integrated EMG activity was less than 5% of activity during stance for all speeds of level running. The springlike behavior of the elements that hold sarcomeres and muscle fibers together has been described in vitro (10), but a functional role for passive muscle elasticity in locomotion has not been demonstrated.

Most of the muscle activity and force production occurred during stance, when force must be produced to support the animal's weight and work must be done to lift and reaccelerate the body. During level running, the muscle provided high forces (up to 35% of peak isometric force at the fastest speed) with small length changes during the stance phase (Fig. 2A). At the fastest running speed, the muscle shortened by $6.6 \pm 1.9\%$ of its resting length. Much of this shortening occurred early or late in the force-producing period, and the work output of the muscle during shortening was less than 3 J kg^{-1} at the fastest running speed (11). Tendon energy storage and recovery provided more than 60% of the work of the muscle-tendon unit (Fig. 3). Most of this energy storage must have occurred in tendon aponeurosis, as the majority of the free tendon is calcified and too stiff to store significant energy (12).

Passive elastic mechanisms can only return energy stored previously in a step, therefore the incremental increase in the potential energy of the body that occurs with each step of incline running must be done by active muscle work. When turkeys ran on inclined treadmills, the work performed by active muscle increased in proportion to the incline (Fig. 4). The force required to support body weight is independent of incline. At a given speed, peak muscle forces were the same for all in-

Fig. 1. Location of force and length transducers implanted in the lateral gastrocnemius muscle of wild turkeys. The lateral gastrocnemius is an extensor of the intertarsal (ankle) joint with a small flexor moment at the knee. A region of this tendon is calcified in adult turkeys, allowing the placement of small strain gauges (lower inset) that can be calibrated to measure the force produced by the attached muscle. Muscle fiber length was measured with sonomicrometer crystals (black hemispheres, upper inset; wires are omitted for clarity) attached to stainless-steel holders and sutured with fine silk along muscle fibers. Bipolar EMG electrodes (not shown) were implanted near the sonomicrometer crystals.
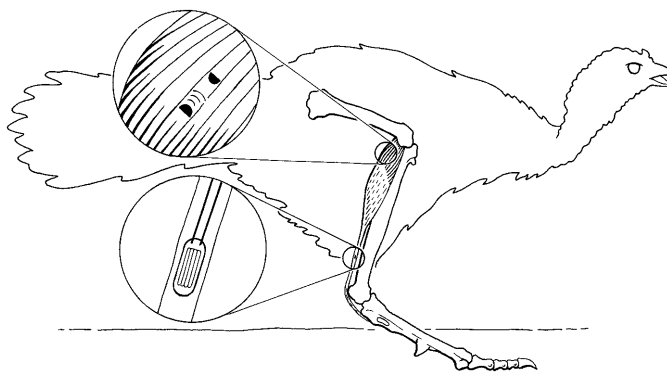
Fig. 2. Fiber length, muscle force, and activity for the lateral gastrocnemius of a turkey running at 3 m s^{-1} on level ground (**A**) and up a 12° incline (**B**). The vertical dashed line indicates when the foot makes contact with the ground. One stride is shown for each incline. During level running, most of the force and activity occur during stance when the muscle shows little length change. Some force is produced passively during the swing phase. During incline running, the muscle shortens more during stance while producing similar force.
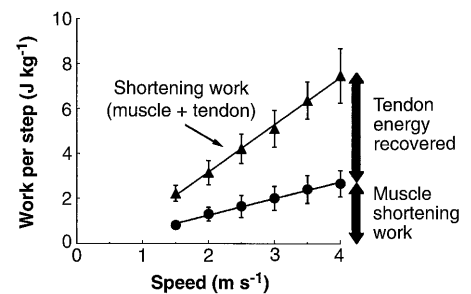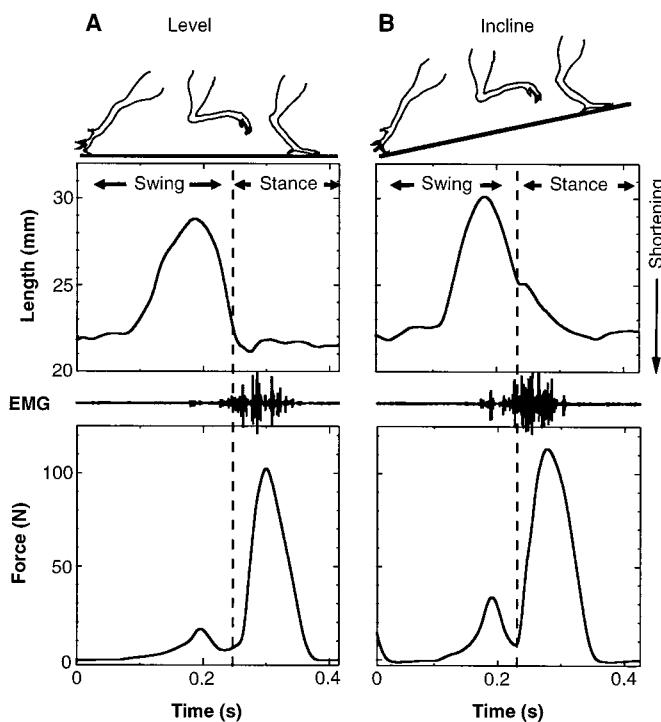

Fig. 3. The work performed during shortening of the lateral gastrocnemius muscle-tendon unit (triangles) and active muscle fibers alone (circles) during stance as a function of speed. Elastic energy recovery from the tendon, the difference between the two lines, accounted for more than 60% of the work during shortening. Work was calculated as the sum of all work performed when the muscle shortened (lengthening work was ignored). Tendon energy recovery was calculated from muscle force and tendon stiffness. Ten strides were analyzed for each animal. Values are the mean and SE for five animals.

clines, and impulse (the area under the force-time relation) increased by less than 30% from 0° to 12° (Figs. 2 and 4). Thus, almost all of the increase in muscle work occurred as a result of increased muscle shortening. The large increase in muscle shortening and work output occurred without a significant change in stance time, indicating that the average rate of shortening increased with incline (13).

What is the energetic benefit of operating muscles to produce force while minimizing work during level running? The increase in muscular work with incline running was paralleled by an increase in the electrical activity in the muscle (Fig. 4) (14). If it is assumed that the integrated EMG is proportional to the number of active muscle fibers, running on a 12° incline required three times the volume of

muscle to produce the same force as that produced during level running (15). These results are consistent with the hypothesis that near-isometric force production during level running increases the force output of active muscle fibers because the muscle contracts over a high force region of its force-velocity curve. Thus, operating muscles at low work outputs during level running increases the force per cross-sectional area of active muscle and allows the runner to support body weight with a smaller active muscle volume.

These results suggest that the skeletal muscle may provide a fundamentally different mechanical function during running than during activities such as swimming, flying, or jumping. These activities require muscle contractions that produce mechanical work at high rates to overcome drag, produce lift, or accelerate the body (16). Because running requires negligible work against drag (17), and the average mechanical energy of the body is constant over time (at a steady speed on level ground), the demands of support may be met most economically by muscles that produce force while minimizing mechanical work.

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5. All animal care and procedures were approved and were in accordance with the animal welfare guidelines of Harvard University. Transducers were surgically implanted in adult wild turkeys (average body mass 3.6 kg). Strain gauges (Tokyo Sokki Kenkyujo Ltd.) were glued to the internal and external aspects of the free calcified tendon with the use of methods developed for bone [A. A. Biewener, *Biomechanics: Structures and Systems* (Oxford Univ. Press, Oxford, 1992)]. Running measurements were made 2 days after surgery. Tendon strain signals were amplified (with a Micromeasurements model 2120 amplifier) and the outputs of the internal and external gauges summed to provide a measure of strain due to muscle tension independent of tendon bending. After the running measurements, animals were anesthetized and strain was calibrated to force in situ with a force transducer (Kistler model 9203). Force had a linear function of strain (correlation coefficient $r^2 = 0.99$; 95% confidence intervals were less than 1% of the slope). The length signal recorded from the sonomicrometer (Triton model 120) was shifted 5 ms to correct for a phase delay. EMG signals were preamplified with DAM50 (World Precision Instruments) differential preamplifiers. All signals were collected at 4000 Hz with a MacAdios II A/D converter. Force and length signals were filtered by software (Superscope II, GW Instruments) with a box-smoothing filter with a cut-off frequency of 150 Hz, and EMG signals were filtered with a high-pass finite impulse response filter with a cut-off frequency of 200 Hz.
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11. Data for the work during shortening are presented because this work is relevant to the energy cost of contraction. The net work done by muscle fibers is equal to the work done by the muscle (during shortening) minus the work done on the muscle (during lengthening). During level running, the muscle also underwent a small amount of active lengthening so that the net work performed by the muscle was not significantly different from zero at all running speeds. Although this result is consistent with the fact that steady-speed running on level ground requires little net work, it is not inevitable; some muscles could perform net positive work while other muscles act as net work absorbers.
12. Although the calcified region of the tendon increases the overall tendon stiffness, considerable soft tendon is available to act as an energy-storing spring. In all, the soft region of the tendon was about 70 mm (including aponeurosis), or about three times the muscle fiber length. Tendon stiffness was determined in anesthetized birds with a method similar to that of Griffiths (7). The leg was immobilized, the muscle was stimulated to contract, and muscle force and length were measured with the implanted transducers. Because the leg was immobilized, the length of the muscle-tendon unit was constant during a contraction, and the measured muscle fiber shortening required an equivalent tendon lengthening (after correction for fiber pinnation angle). This technique had the advantage that the tendon remained intact during the measurements, and the force-length curve produced by this method provides a measure of tendon stiffness that includes the elastic properties of the aponeurosis as well as those of the free tendon.
13. A comparison of the work done at different inclines is a good indicator of the increase in shortening velocity, because at the same speed the stance period occurred over approximately the same amount of time, and the force produced was similar. Direct calculations of the stance shortening velocity would be more difficult to interpret because the velocity is variable during stance of level running, and most of the shortening occurs early or late in stance, when force is low.
14. EMG signals were rectified and integrated over the stance period. EMG values for individual animals were normalized to the value obtained for that animal during level running at the same speed (2.5 m s⁻¹). This normalization accounts for differences in amplitude that occur with variable electrode quality and orientation.
15. An increase in integrated EMG activity could also indicate an increase in repetitive rate of activation of individual motor units [J. V. Basmajian and C. J. DeLuca, *Muscles Alive: Their Functions Revealed by Electromyography* (Williams & Wilkins, Baltimore, MD, 1985)]. This would be an alternative mechanism for increasing the force output of individual fibers, and it would also require a higher rate of energy consumption.
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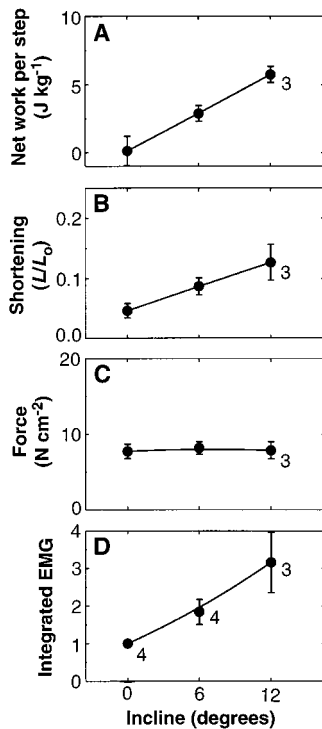
Fig. 4. Net muscle work (**A**), shortening distance (**B**), force (**C**), and activity (**D**) during stance phase of running at three inclines. Significantly more muscle had to be activated, as indicated by the integrated EMG signal, to provide the same level of force as the muscle shortened more during incline running. The running speed was 2.5 m s⁻¹ for all inclines. Fractional shortening (L/L_0) was determined as the initial length minus the final length during stance force production L, divided by the length at initial foot contact (separate experiments indicate that the length at foot contact is a close approximation of the length at which isometric force reaches a maximum, L_0). All parameters changed significantly with incline (two-factor analysis of variance with factors of individual and slope, $P < 0.03$) except muscle force. Values shown are the mean ± SE for the number of animals indicated beside each point or for five animals if no number is indicated.