

Adjusting muscle function to demand: joint work during acceleration in wild turkeys

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Summary

We measured the net work performed at hind limb joints in running turkeys to determine the source of mechanical power for acceleration. We tested the hypothesis that net mechanical work per step increases in proportion to acceleration at all four major hind limb joints (hip, knee, ankle and tarsometatarsal–phalangeal joint). This hypothesis was based on the idea that all hind limb muscles should contribute mechanical work to maximize performance during accelerations, and a previous study that indicated the mechanical power output of the entire turkey hind limb musculature was remarkably high. We used high-speed video and force-plate measurements to measure joint moment, velocity and power output during single foot-contacts of running accelerations. By measuring steps in which the animals were relatively more or less motivated to accelerate, we obtained data for a range of accelerations, all at approximately the same running speed. Net joint work per step increased at the hip and ankle as a function of acceleration. Hip net work per unit body mass was $0.12 \pm 0.09 \text{ J kg}^{-1}$ averaged over the five lowest accelerations ($-0.22 \pm 0.08 \text{ m s}^{-2}$), and $0.87 \pm 0.20 \text{ J kg}^{-1}$ for the five highest accelerations ($4.86 \pm 0.27 \text{ m s}^{-2}$). Ankle work was $-0.21 \pm 0.11 \text{ J kg}^{-1}$ for the lowest accelerations and $0.71 \pm 0.28 \text{ J kg}^{-1}$ for the highest. The high work output at the ankle is consistent with the idea that elastic

mechanisms function to increase muscle work during acceleration. The work performed at the knee and tarsometatarsal–phalangeal joint was independent of acceleration in a step. These results support the idea that hip and ankle extensors contribute significantly to the work necessary to accelerate the body.

We also measured the change in joint moment and angular excursion with acceleration to determine whether the mechanism for increasing work output at a joint involved an increase in muscle force or muscle shortening. The increase in joint work at the hip and ankle resulted almost entirely from an increase in joint angular excursion during stance. Hip extension increased by more than threefold from the lowest to the highest accelerations, and the angular excursion of the ankle increased from $-24.8 \pm 4.7^\circ$ (net flexion) at the lowest accelerations to $33.0 \pm 12.8^\circ$ (net extension) at the highest accelerations. Mean stance joint moment was unchanged with acceleration at the ankle and increased by approximately 35% at the hip across the range of accelerations. These patterns of joint moment and excursion indicate that turkeys increase mechanical work for acceleration primarily by increasing muscle shortening, rather than muscle force.

Key words: locomotion, muscle work, muscle power, avian, running.

Introduction

One of the remarkable features of the musculoskeletal system is its ability to adapt to the varied mechanical demands of different movements. This challenge may be particularly significant in terrestrial locomotion, where the demand for mechanical work can vary widely with surface slope, substrate, or fluctuations in center of mass velocity. Most of what we know about muscle function during running comes from studies of steady-speed movement on level ground, when the demand for mechanical work is nearly zero. The muscular system does some negative work (energy absorption) and positive work (energy production) during

each step, but the net work output must be zero if an animal's speed and elevation are unchanged from stride to stride. During steady-speed running, many muscle–tendon units act as springs, storing and recovering mechanical energy with each step to minimize the cyclic work that must be done by active muscle contractions (Cavagna et al., 1964; Alexander, 1988; Taylor, 1994; Roberts et al., 1997). By contrast, a burst of acceleration requires muscles to shorten to perform the work of increasing the body's kinetic energy. Because the vast majority of studies of terrestrial locomotion focus on steady-speed movement, we know very little about how

muscles transition from the spring-like function of steady-speed running to the motor-like function required for acceleration.

We measured the moment of force, power and velocity at individual joints in accelerating turkeys to address two questions. First, where is the power for acceleration developed? Previously we found very high power outputs of the entire hind limb (Roberts and Scales, 2002), and therefore we predicted that work output of all hind limb joints would increase with increasing acceleration. Alternatively, high-power activities like acceleration might be powered by only a subset of limb muscles. For example, there is evidence that dogs recruit longer-fibered more-proximal muscles to power jumping, while the ankle extensor muscle–tendon units provide the same spring-like function during both jumping and galloping (Alexander, 1974). The second question motivating our study was, how is muscle work increased at individual joints? Work is the product of force and displacement, and the joint work performed during stance could be increased by increasing one or both of these variables. We predicted that joint work would increase primarily as a result of increases in joint excursion. This prediction was based on measurements of force and strain in individual muscles, which indicate that for several muscles an increase in muscle work from level to incline running is achieved primarily by an increase in muscle shortening (Roberts et al., 1997; Daley and Biewener, 2003; Gabaldon et al., 2004).

We measured joint mechanics during single footfalls as turkeys ran across a force-plate in a trackway. Strides for analysis were chosen that were all approximately the same running speed, but varied in the amount the animal accelerated during the step. Joint moment, angle and power were measured by high-speed video and force-plate measurements using inverse dynamics. We tested two hypotheses: (1) work output increases at all major joints in direct proportion to acceleration and (2) any increase in work is due to an increase in the net joint angular excursion.

Materials and methods

Animals and running protocol

Five adult eastern wild turkeys (*Meleagris gallopavo* L.) were obtained from a local breeder. Two males and three females were used in this study. The mean body mass of the animals was 3.08 ± 0.27 kg. Animals were maintained in a large indoor enclosure at approximately 20°C and fed food and water *ad libitum*. All procedures and animal care were approved by the Oregon State University Institutional Animal Care and Use Committee.

The running protocol has been described in detail previously (Roberts and Scales, 2002). Force and video measurements were recorded from single footfalls as animals ran over a trackway at mean speeds of 1.75–2.25 m s⁻¹. A total of 49 runs over a wide range of accelerations was recorded. The mean stance horizontal force divided by body mass was used as a

measure of acceleration. Runs were chosen for analysis such that data for individual birds were evenly distributed across the range of accelerations.

Force measurements

A piezoelectric force-plate (Kistler 9233aa; Kistler USA, Amherst, NY, USA) placed in the trackway was used to measure ground reaction force magnitude and position during single footfalls. Force-plate signals were acquired to computer at 1000 Hz with a 12-bit A/D board (National Instruments PCI-MIO-16E-1) using Labview (National Instruments, Austin, TX, USA) software. The start of video and force acquisition was triggered from an external signal to allow synchronization of the two signals. Force data were smoothed in software with a bidirectional low-pass Butterworth filter with a 100 Hz cut-off frequency.

Video measurements

Joint positions in a sagittal plane were determined from high-speed video recordings (Redlake Motionscope 1000, San Diego, CA, USA). Small reflective markers (3M; 70610WS) were applied to the skin. Markers were applied at the center of rotation of the tarsometatarsal–phalangeal (TMP) joint and the ankle (intertarsal) joint. Knee and hip centers of rotation could not be marked directly because the wing obstructed the view of the hip, and knee movement occurred independently of skin movement. To locate the position of the knee in the video, two markers were placed along the tibiotarsus at about a third and two-thirds the distance from the ankle to the knee. These markers were aligned such that the position of the knee center of rotation could be extrapolated from the position of the ankle marker and the known distance from the ankle to the center of rotation of the knee. A similar technique was used to determine the position of the hip using a marker glued to the back of the animal just above the hip. Because there is virtually no movement of the skin on the back, this marker was fixed relative to the acetabulum, thus providing a good indicator of the position of the center of rotation of the hip. These methods for determining joint centers of rotation have been validated previously using high-speed x-ray cine analysis, which indicated that the largest error in joint marking occurs at the most proximal joints and is less than 0.5 cm (Roberts et al., 1998). To determine the rotation of the body (for the calculation of hip angle), two markers were attached along the back of the animal.

Video data was captured into a Macintosh Computer using a Scion LG-3 frame-grabbing card. Marker positions were digitized using a custom-designed macro written for NIH Object-Image (a version of NIH Image adapted by Norbert Vischer; <http://simon.bio.uva.nl/object-image.html>). Joint position data were smoothed in software using a cubic spline interpolation available in Wavemetrics Igor (smoothing factor=1, s.d.=0.001). Joint position data and force data were combined in software (Microsoft Excel and Wavemetrics Igor) for calculation of joint moments and powers.

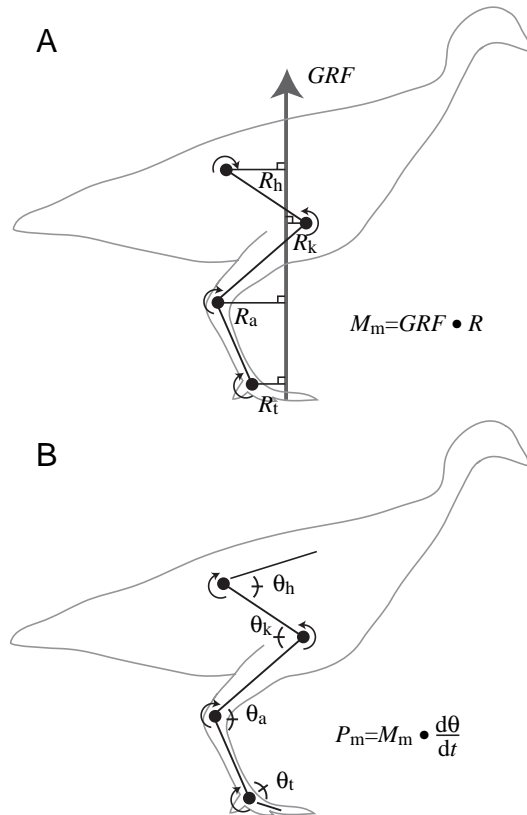


Fig. 1. The method for calculating joint moments, M , and powers, P_m . Joint moment (A) is the product of the magnitude of the ground reaction force, GRF , and the out-moment arm, R . R is the orthogonal distance from the GRF to the center of rotation of the joint. Arrows indicate the direction of positive net moments produced by muscles at a joint. Joint angles were measured as indicated in B. Joint velocities were calculated from the time derivative of the angle (θ) change. The arrows denote the direction of positive velocities. Definitions: a, ankle; h, hip; k, knee; t, toe.

Net muscle moment, velocity and power

Net muscle moments (M_m) were determined from the ground reaction force (GRF) and joint positions as illustrated in Fig. 1. The net muscle moment is calculated from the product of the GRF , and the joint out-moment arm (R) (the orthogonal distance from the GRF to the center of rotation of the joint; Biewener, 1989):

$$M_m = GRF \cdot R. \quad (1)$$

By convention, we assigned positive values to moments produced by muscles that tend to support body weight during normal standing. Thus, positive moments represented net extensor muscle moments for the hip, knee and ankle. At the toe, flexion supports body weight and has the potential to contribute positive power to lift and accelerate the body, therefore net flexor muscle moments at the TMP joint were considered positive. Muscle moments necessary to accelerate the limbs relative to the body and to balance gravitational forces on the limbs were not calculated. These moments are

expected to be negligible at more distal joints and small at proximal joints in birds (Clark and Alexander, 1975). These moments also do not contribute to accelerating the center of mass of the animal.

Joint angles were determined from joint position data as shown in Fig. 1. To determine the extension of the femur at the hip, we calculated the sum of the angle of the femur to the horizontal and the angle of the back relative to the horizontal. This assumes that changes in the back angle accurately represent changes in pelvic angle. Joint velocity was calculated from the time derivative of joint angle using the differentiation function in Wavemetrics Igor (central-point difference differentiation). The sign conventions used for joint velocities were the same as those for joint moment: positive velocities at the hip, knee and ankle were recorded when the joints were extending, while positive velocities at the TMP joint represented joint flexion.

The mechanical power developed at a joint, P_m , is equal to the product of the net muscle moment, M_m and the joint velocity, ω :

$$P_m = M_m \cdot \omega. \quad (2)$$

Positive power (work performed by muscles) is developed when the sign of the moment and the velocity are the same, i.e. net muscle extensor moments are produced while the joint extends or muscle flexor moments are produced as the joint flexes. Negative work (energy absorbed at a joint) is performed when the joint velocity and moment have opposite signs, i.e. the joint flexes as extensor muscles produce force. It is important to note that the calculated joint powers represent the power produced at a joint, but not necessarily the power developed by the muscles at that joint. Muscles that cross more than one joint can act to transfer power from one joint to another (van Ingen Schenau et al., 1992; Jacobs et al., 1993). Thus, the power measured at a given joint represents the sum of the power applied directly by muscles at that joint as well as power transferred from other joints.

The net work performed at a joint during stance was calculated from the area under the power–time curve for that joint. Positive power outputs represent positive work (work done by muscle–tendon units) and negative power outputs represent negative work (work absorbed by muscle–tendon units). Elastic elements can store and recover energy but they cannot perform net work. Thus, we assumed that net work performed during an entire step was equal to the net work performed by muscle contractile elements.

The total work done on the center of mass (COM) during a step was determined from force-plate ergometry (Cavagna et al., 1964). A detailed description of these methods has been presented previously (Roberts and Scales, 2002).

Least-squares linear regression was used to determine the effect of acceleration on variables of interest. The criteria for significance was $P < 0.05$. It was determined by ANCOVA (analysis of covariance) that there was no significant effect of individual bird on any of the values measured. Therefore, data for individual birds were pooled for least-squares regressions.

Results

Joint work

Fig. 2 presents the sum of the work measured at the hip, knee, ankle and TMP joint as a function of the work done on the center of mass during a step. The center of mass work is a measure of the work done on the body, calculated from force-plate ergometry (Roberts and Scales, 2002), while the joint work is the sum of the mechanical work performed at the hind limb joints. The sum joint work, as measured by our methods, should be very nearly equal to the work done to move the center of mass. The deviation of measured values from this line of unity primarily represents measurement error. Both center of mass and joint work rely on the measurement of the ground reaction force, but only joint work measurements use high-speed video measurements of joint positions. Measurements of joint work are particularly sensitive to errors in locating and digitizing the center of rotation of the joints. Because joint work is determined from the product of joint moment and joint angular displacement, any error in joint location determination is multiplied during calculations of joint work.

Work output at the hip and ankle increased with acceleration, while knee and TMP work was unchanged (Fig. 3). Hip work and ankle work increased at about the same rate with increases in acceleration (the slope of the regression of net work *versus* acceleration was 0.154 ± 0.017 for the hip and 0.192 ± 0.012 for the ankle). The extensor muscle mass at the hip is nearly equal to that of the ankle (Roberts et al., 1998). Thus, the contribution of work from the hip and the ankle is approximately in proportion to the extensor muscle mass at these joints. Work output at the knee was most frequently positive but was independent of acceleration.

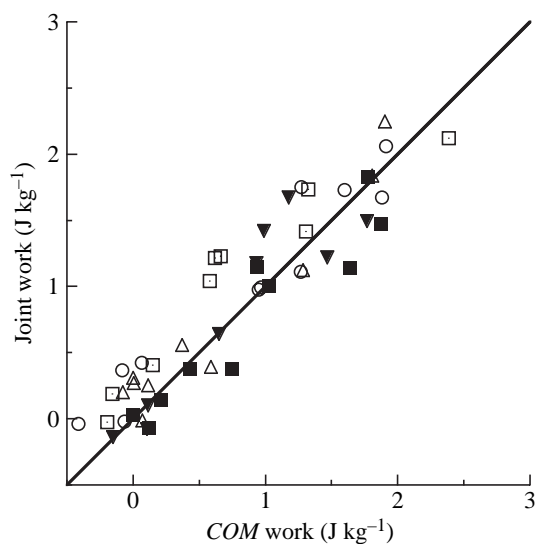


Fig. 2. The sum of the measured joint work values, calculated from inverse dynamics, *versus* the work required to move the center of mass (COM) of the body calculated from force-plate ergometry. The line indicates unity. Different symbols identify individual birds.

Joint moment and excursion

To determine whether muscle work output was increased by increasing the force that muscles developed, or the distance over which they shortened, we measured changes in joint moment and angular excursion for each joint as a function of acceleration. There was a small but significant increase in mean joint moment with acceleration for all joints except the ankle (Fig. 4). To determine whether the changes in joint moment with acceleration resulted from a change in ground reaction force or a change in mean joint mechanical advantage (Equation 1), we estimated the mean moment arm of the ground reaction force (R) during stance. Because the knee produces both net flexor and extensor moments during stance, we measured the mean moment arm for flexion and extension

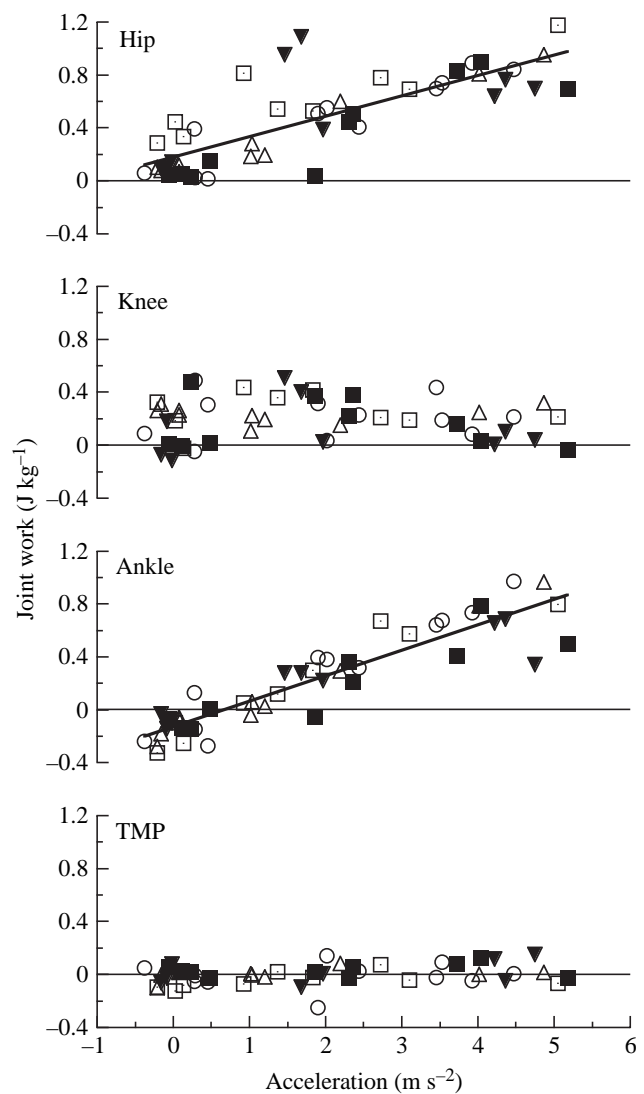


Fig. 3. As acceleration increased, the net work per kg body mass performed during a single step increased at the hip and the ankle. Net work was independent of acceleration at the knee and the tarsometatarsal-phalangeal (TMP) joint. Linear regressions ($N=49$) are shown for hip, $y=0.154x+0.177$, $r^2=0.64$, $P<0.01$; ankle, $y=0.192x-0.129$, $r^2=0.84$, $P<0.01$.

separately for the knee. There was a significant change in mean moment arm during a step for negative (flexor) moments at the knee (Fig. 5). The regression of hip R on acceleration also produced a significant slope.

There was a significant increase in the net joint excursion (angle at toe-off minus angle at toe-down) at the hip, knee and ankle (Fig. 6). A comparison of values for the five lowest accelerations ($-0.22 \pm 0.08 \text{ m s}^{-2}$, approximately steady speed) and the five highest accelerations ($4.86 \pm 0.27 \text{ m s}^{-2}$) indicates that net hip extension approximately tripled from steady speed to the highest accelerations ($10.3 \pm 7.9^\circ$ versus $34.5 \pm 13.2^\circ$). The mean ankle angular excursion for the five lowest accelerations was $-24.8 \pm 4.7^\circ$ (net flexion) versus $33.0 \pm 12.8^\circ$ (net extension) for the five highest accelerations. Because these joints produce positive extensor moments of force, increases in net extension result in increases in positive work. As acceleration increased, the net flexion at the knee decreased. The reduction in knee

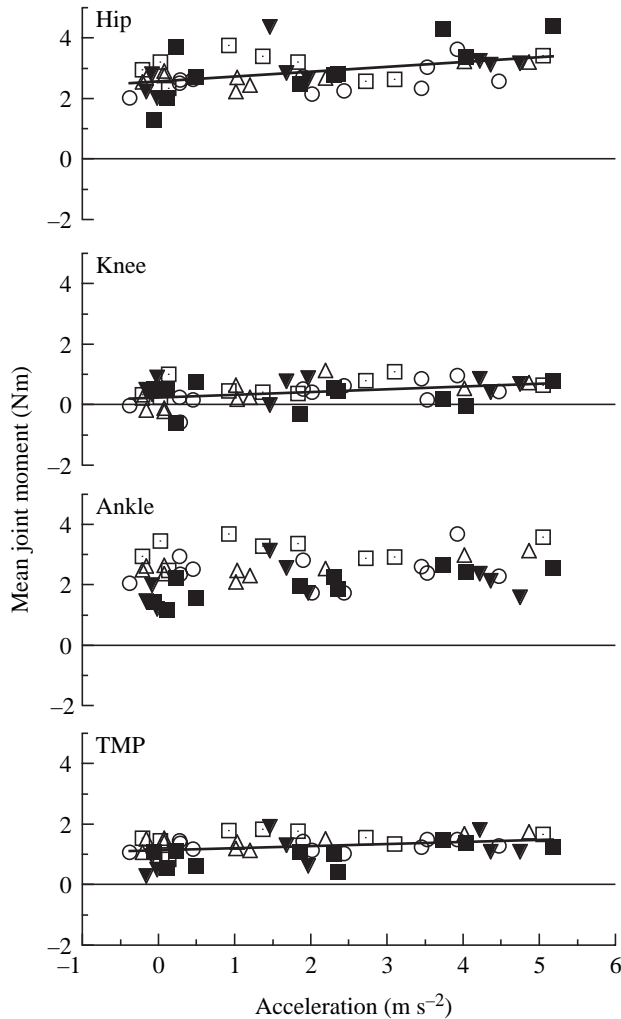


Fig. 4. The mean moment produced at each joint during stance showed a small but significant increase with acceleration at all joints except the ankle. Linear regressions ($N=49$) are: hip, $y=0.16x+2.55$, $r^2=0.20$, $P<0.01$; knee, $y=-0.09x+0.24$, $r^2=0.14$, $P<0.01$; TMP, $y=0.06x+1.14$; $r^2=0.05$, $P<0.05$.

flexion may be related to the need to reduce leg protraction angle during the stance phase of accelerations (Roberts and Scales, 2002), as much of the reduction in knee flexion resulted from a decrease in knee angle at toe-down.

Figs 7–10 present joint moment, angle and power for representative steps for zero (steady-speed), moderate and high acceleration. Fig. 7 illustrates that although a relatively large moment was produced at the hip, power and work (the area under the power curve) during steady-speed running were low because of the limited excursion at this joint in avian runners (Gatesy, 1999). Power output increased with acceleration as the joint extended more during force production. At all accelerations, the work absorbed at the hip (area under the negative portion of the power curve) was small because the

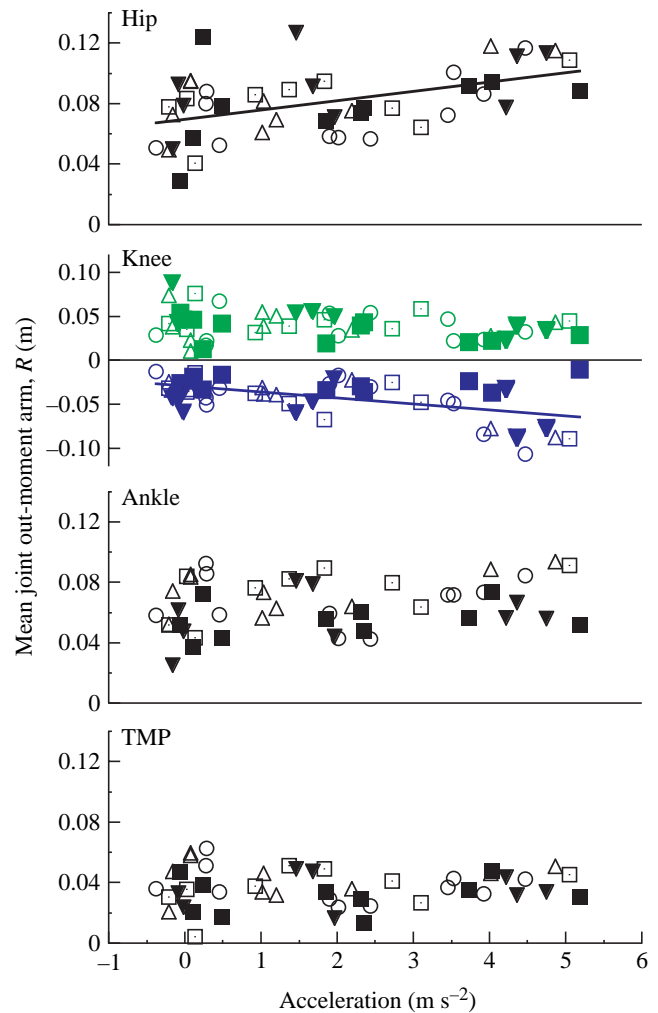


Fig. 5. The moment arm of the ground reaction force (R ; Fig. 1) averaged over the step did not change with acceleration at the ankle or tarsometatarsal–phalangeal joint. Hip moment arm increased with acceleration ($y=0.0061x+0.069$, $r^2=0.23$, $P<0.001$). Mean moment arms during knee extension (green) and knee flexion (blue) were measured separately. Only the mean flexion moment arm at the knee changed significantly with acceleration. Linear regression for the knee flexion moment arm was $y=-0.0070x-0.029$, $r^2=0.27$, $P<0.05$.

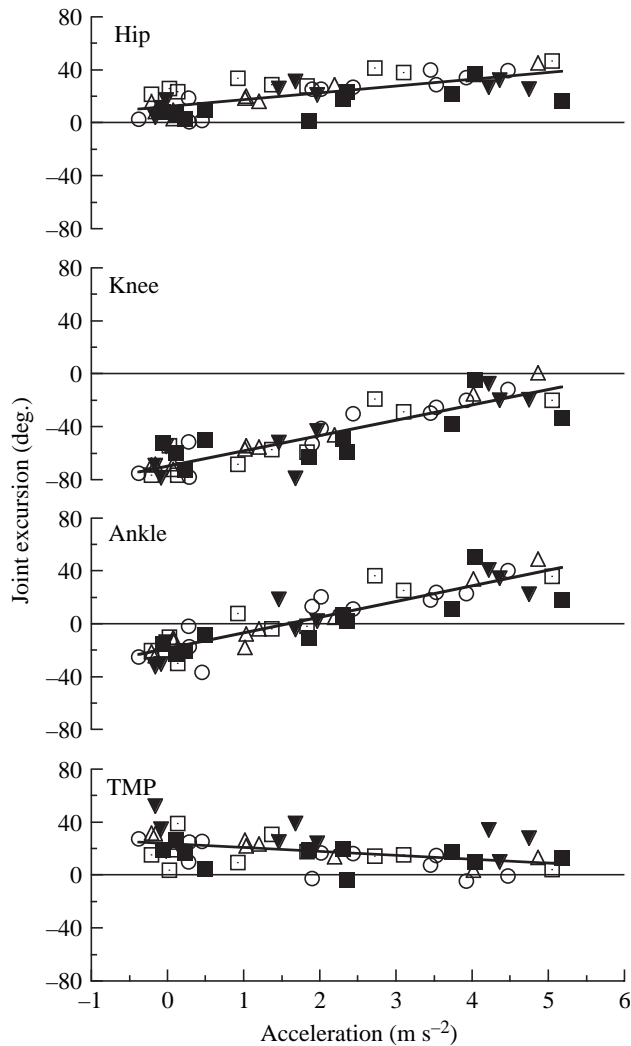


Fig. 6. The net excursion at a joint during a single step, measured from the difference between angle at toe-down and angle at toe-off, as a function of acceleration. Positive values indicate net joint extension and negative numbers indicate joint flexion. The hip and the ankle extended more as acceleration increased, while the knee underwent less flexion. The tarsometatarsal-phalangeal (TMP) joint extended less as acceleration increased. Linear regressions ($N=49$) are shown for hip extension, $y=5.13x+12.3$, $r^2=0.51$, $P<0.01$; knee, $y=11.52x-69.64$, $r^2=0.76$, $P<0.01$; ankle, $y=11.93x-18.98$, $r^2=0.80$, $P<0.01$; TMP, $y=-2.98x+23.85$, $r^2=0.19$, $P<0.01$.

flexion at the joint was small. The high power produced late in stance during accelerations was associated with a shift in timing of force production, from early to mid-stance during steady-speed running to late stance for acceleration. The time of peak joint moment, expressed as a fraction of total contact time, increased significantly with acceleration (linear regression, $y=0.322+0.042x$; $r^2=0.51$, $P<0.01$). Late stance force production coincided with the period of the most rapid extension of the hip, explaining in part the increase in power and work from steady speed to acceleration.

The power profile at the knee was complex (Fig. 8). Early

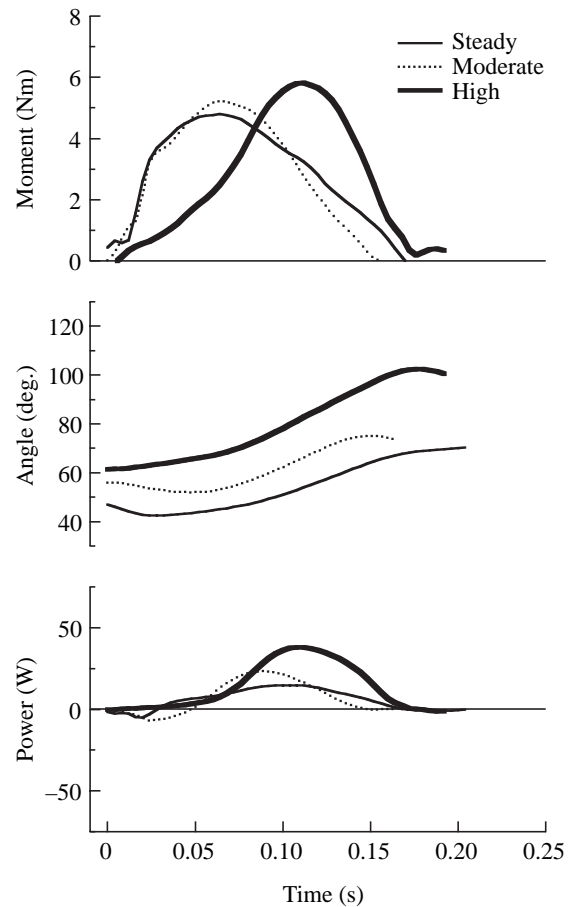


Fig. 7. Hip joint moment, angle and power during single footfalls for three representative strides during a steady-speed run, a moderate acceleration and a high acceleration (mean acceleration during stance= 0.13 m s^{-2} , 2.31 m s^{-2} , and 4.47 m s^{-2} respectively). Angles and moments are measured as indicated in Fig. 1. The area under the positive power curve represents work done at the joint, while the area above the negative region of the power curve is work done on the joint.

in the stride, the knee produced a net flexor moment at the same time that it flexed, to result in positive power. The knee also produced some positive power later in the step, when it produced an extensor moment as it extended. The initial flexion of the joint decreased with acceleration, resulting in a small decrease in power output during this portion of the step. Joint moment profiles were similar at all accelerations.

Net power (or work) output at the ankle increased with acceleration because the energy absorbed at the joint (negative power) decreased, and the power produced increased (Fig. 9). Generally, as acceleration increased, the ankle was more flexed at toe-down and more extended at toe-off. It tended to flex to the same minimum angle at all accelerations. Joint moments changed with acceleration, but this change was small relative to the change in joint excursion. As with the hip, the time of peak joint moment, expressed as a fraction of total contact time, increased significantly with acceleration (linear regression, $y=0.38+0.036x$; $r^2=0.46$, $P<0.01$).

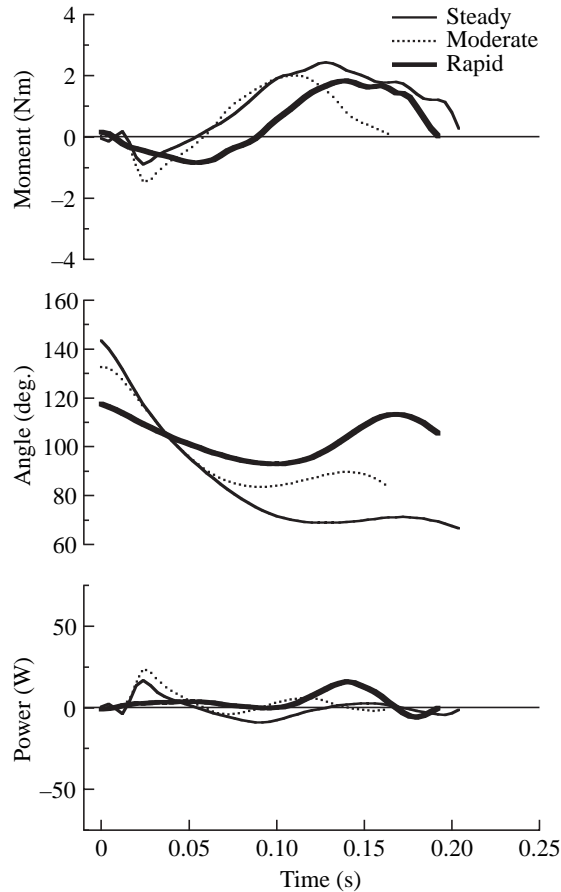


Fig. 8. Knee joint moment, angle and power during foot contact for the three representative steps shown in Fig. 7.

The TMP produced a brief burst of positive power during rapid extension in late stance (Fig. 10). This positive power was generally balanced by negative power earlier in stance to result in no net work.

Discussion

The source of work for acceleration

The mechanical work for acceleration in running turkeys is performed primarily by forceful extension of the hip and ankle joints. Work increased at both joints in direct proportion to acceleration, and the contribution of net work at the two joints was approximately equal. At the knee and TMP joint, there was no significant change in joint work with acceleration. Thus, our hypothesis that mechanical work would increase at all joints in proportion to acceleration is not supported.

The high work and power outputs measured at the ankle and hip during accelerations indicate high power and work outputs of the extensors of those joints. This conclusion requires the assumption that the power measured at the ankle and the hip was not produced by extensors at another joint (e.g. the knee) and transferred *via* biarticular muscles (van Ingen Schenau et al., 1992). Transfer of power between joints has been demonstrated in studies of human jumping, where much of the

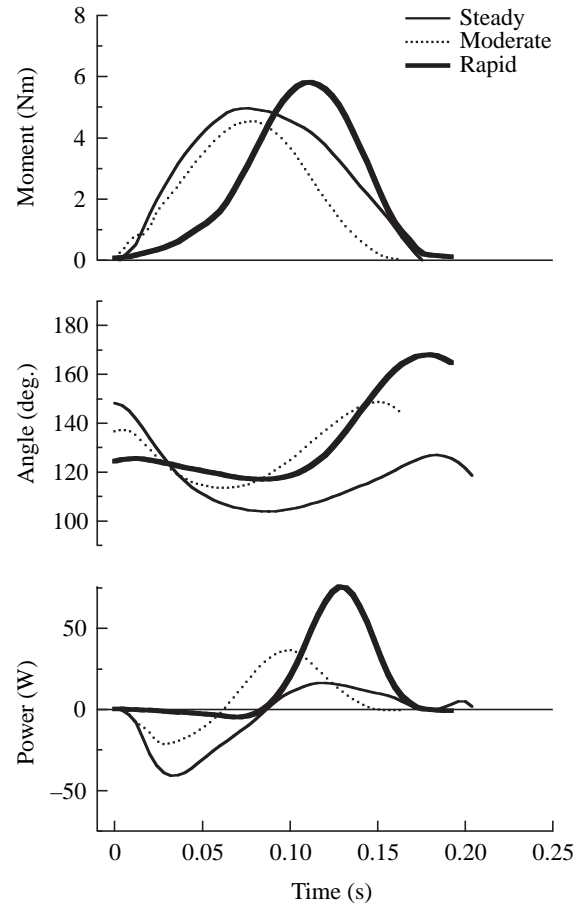


Fig. 9. Ankle joint moment, angle and power for the three representative steps shown in Fig. 7.

power developed at the ankle results from a transfer of power from knee extensors to the ankle via the biarticular triceps surae (Bobbert et al., 1986). Transfer of mechanical power *via* analogous biarticular linkages is possible in avian runners. However, we believe that the conclusion that hip and ankle powers measured in the present study reflect power generated primarily by the extensors of those joints is justified by a consideration of avian limb anatomy. The muscle mass of knee extensors in birds is too small to account for the very high mechanical work measured at the ankle during high accelerations. The knee extensor muscle mass in a single limb is only 0.7% of body mass, while ankle extensors represent 2.5% of body mass (Roberts et al., 1998). The work done at the ankle during the most rapid accelerations, approximately 0.8 J kg^{-1} body mass, would require a work output of 114 J kg^{-1} muscle if transfer of power from knee extensors provided all of this work. Power can be transferred only while the knee is extending, and this occurs only for approximately 70 ms in rapid accelerations. To produce the work performed at the ankle in this amount of time, the knee extensors would have to develop a mean power in this period of more than 1600 W kg^{-1} . Similarly high values of muscle work and power would be necessary if the work measured at the hip were supplied by knee

extensors. The estimate of 114 J kg^{-1} is nearly double the estimated maximum capacity for work production of rapidly contracting vertebrate skeletal muscle (Peplowski and Marsh, 1997), and 1600 W kg^{-1} is approximately $4\times$ the maximum power output of turkey hind limb muscle (Nelson et al., 2004). Thus, while transfer of power from knee extensors may occur, it cannot explain the high work outputs measured at the hip and ankle during accelerations.

The relatively short fibers and long tendons of turkey ankle extensors are features typically associated with a spring-like function for running (Ker et al., 1988). The stretch and recoil of tendon springs can allow active muscle fibers to produce force while undergoing little change in length. These low-work contractions reduce metabolic cost. Short fibers also improve the economy of force production in these muscles, because a smaller volume of muscle must be active per unit force produced (Rall, 1985; Biewener and Roberts, 2000). The results from the present study indicate that in running turkeys, ankle extensors that act as effective springs during steady-speed running can also effectively perform net mechanical work for accelerations. These results are not consistent with the idea that architectural features of spring-like muscles limit their ability to develop mechanical work.

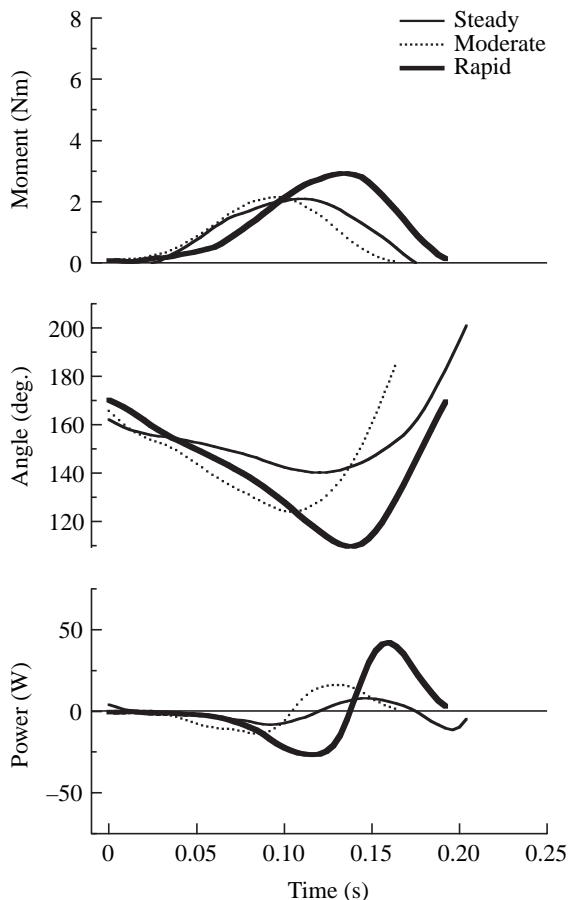


Fig. 10. Tarsometatarsal–phalangeal joint moment, angle and power for the three representative steps shown in Fig. 7.

Models of muscle contraction during acceleration suggest that the stretch and recoil of tendon springs may facilitate high muscle power outputs by allowing muscle contractile elements to contract at relatively constant velocities (Roberts, 2002). The energy stored in a muscle's tendon depends only upon the force that is applied to it. Thus, during both acceleration and steady-speed running, tendons store and recover mechanical work as force rises and falls with each stance period. During steady-speed running, the source of the stored elastic energy is primarily the decline in potential and kinetic energy of the body during the first half of the step. At the level of the joint, this is apparent in negative power during, for example, ankle flexion (Fig. 8). The negligible negative power observed at the ankle during rapid accelerations suggests that energy that must be loaded into tendons during the first half of the step comes directly from shortening muscle contractile elements. These two different mechanisms – storage and recovery of mechanical work of the body *versus* storage and recovery directly of muscle work – reflect the different roles that elastic mechanisms play during steady-speed running *versus* acceleration. During steady-speed running elastic mechanisms improve metabolic economy by reducing muscular work, while during maximal accelerations the stretch and recoil of elastic elements redistributes in time the application of muscle power to the body. The redistribution of muscle power by elastic mechanisms in the turkey ankle extensors may actually enhance a muscle's ability to develop power, because it may allow the muscle to contract at a relatively constant velocity and power output even when the velocity and power of the joint fluctuate (Roberts, 2002). The favorable effects of elastic energy storage and recovery on muscle power development that have been observed for jumping (Bobbert et al., 1986; Alexander, 1995; Aerts, 1997; Roberts and Marsh, 2003), may apply generally to muscle-powered accelerations.

Mechanisms for altering hip and ankle net work

How is muscle work output increased from steady-speed running to acceleration? The work performed during a muscle contraction is the product of the muscle force and the distance shortened. In the transition from steady-speed running to acceleration, the increase in net work might be achieved by an increase in the force output of muscles that undergo significant shortening during steady-speed running. Alternatively, muscles that produce force during steady-speed running could shorten more to provide net work for acceleration. Either of these strategies would be apparent in an increase in joint moments or joint excursion, respectively.

The primary mechanism for increasing the mechanical work output of the turkey hind limb musculature from steady-speed running to acceleration was an increase in joint angular excursion, rather than joint moment. Joint moment was unchanged with acceleration at the ankle and increased by approximately 35% at the hip from the lowest to the highest accelerations. By contrast, hip net extension during stance increased more than threefold from the lowest to the highest accelerations, and ankle excursion increased from a net flexion

of $-24.8 \pm 4.7^\circ$ to $33.0 \pm 12.8^\circ$ net extension. At the ankle, this increase in net excursion during stance resulted from both an increase in joint extension and a decrease in joint flexion (Fig. 9). If we assume that muscle shortening is proportional to net joint excursion and muscle forces are proportional to joint moments, these results indicate that the primary mechanism for increasing mechanical work output from steady-speed running to accelerations is an increase in muscle shortening, rather than an increase in muscle force.

The pattern of joint moment observed during accelerations also suggests that a change in timing of force production may play a role in increasing joint work. Hip and ankle moments reached a maximum at approximately mid-stance during steady-speed runs (Figs 7, 9). During accelerations, peak moments occurred late in stance, corresponding to the period of rapid joint extension. Because joint power is the product of joint velocity and moment, this shift in the timing of joint moment resulted in an increase in joint power. A similar mechanism for altering power output has been observed in individual muscles of guinea fowl and turkeys running on different inclines (Daley and Biewener, 2003; Gabaldon et al., 2004).

We were interested in determining whether mechanical advantage was altered from steady-speed running to acceleration because we expected that the change in orientation of the ground reaction force associated with acceleration (Roberts and Scales, 2002) would result in a change in R , the distance from the GRF vector to the joint center of rotation (see Fig. 1). The mechanical advantage can be defined as the ratio of the muscle moment arm and the GRF moment arm, R . A difference in mechanical advantage has been observed at the ankle in humans running at a steady speed *versus* accelerating (Carrier et al., 1994). Of the joints that contributed work to acceleration in our study, only the hip showed a significant change in step-averaged R across the range of accelerations. The small increase in muscle moment at the hip resulted from both an increase in GRF magnitude and a change in R (see equation 1). The contribution of possible differences in muscle moment arm to changes in mechanical advantage during steady-speed running *versus* acceleration was not estimated in this study. Mechanical advantage might also be influenced by differences in muscle moment arm between conditions, as the ankle and hip operated at different joint angles for steady-speed running and accelerations.

Variation in the mechanical advantage during the course of a step may also influence muscle function. Carrier et al. (1994) found that the mechanical advantage of the ankle extensors in running humans decreased throughout the foot contact period, reducing the variation in muscle velocity during the step. We also observed differences in the pattern of R that reflect possible differences in mechanical advantage between steady-speed running and acceleration. During accelerations, the change in R during a step at the ankle indicates that mechanical advantage increased steadily throughout the contraction (Fig. 11). This pattern is the opposite of that observed in running humans, and would presumably be unfavorable for

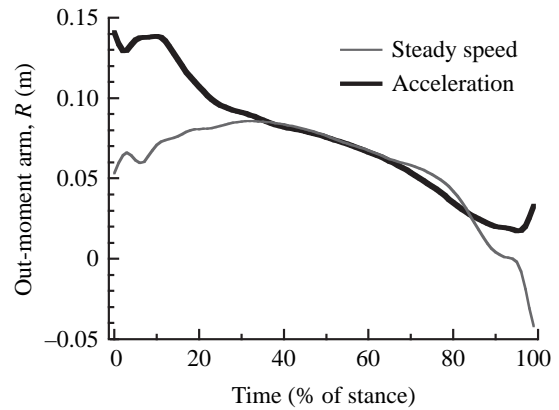


Fig. 11. Ankle out-moment arm, R , *versus* time of stance, averaged for the five highest accelerations (thick line) and the five lowest (thin line, approximately steady speed). Mean values for individual trials were calculated after normalizing for stride time.

muscle contractile units operating alone. However, modeling of muscle-powered accelerations suggests that when muscles operate in series with significant elastic elements, muscle work may be maximized when the muscle operates through a continuously increasing mechanical advantage (Roberts and Marsh, 2003). The pattern of increasing mechanical advantage observed for accelerating turkeys may therefore reflect a variable leverage that operates to allow effective storage and release of elastic strain energy during each step.

Muscle shortening velocity for acceleration versus steady-speed running

The changes in joint moment and excursion with increasing acceleration in turkeys suggest that, generally, muscles produce similar forces for both steady-speed running and acceleration, but they operate at different shortening velocities. This conclusion is based upon a comparison of accelerative and steady-speed steps at a single running velocity. The increase in joint excursion over approximately the same contact time from steady-speed running to acceleration suggests that muscle shortening velocity, V/V_{\max} , increases with acceleration. This is consistent with the behavior of a model of muscle-tendon unit action during acceleration, where a doubling of the volume of muscle recruited to accelerate a load resulted in a large increase in muscle shortening velocity and only a small increase in muscle force (Roberts, 2002). Measurements of individual muscle function suggest that a similar mechanism explains the increase in muscle work from level to uphill running. Muscle work, shortening and integrated EMG all increase as a function of incline in the lateral gastrocnemius muscle of running turkeys, while the peak force produced remains unchanged (Roberts et al., 1997). This change in muscle shortening and work output may be facilitated by elastic mechanisms. Together, these results support the idea that steady speed, level running can be characterized as a low mechanical power activity, where muscles operate effectively at low V/V_{\max} values, whereas acceleration may be

characterized as a high-power activity, where muscles operate at intermediate V/V_{\max} values favorable for muscle power production.

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