EXTERNAL WORK AND POTENTIAL FOR ELASTIC STORAGE AT THE LIMB JOINTS OF RUNNING DOGS

COLIN S. GREGERSEN, NATALIE A. SILVERTON AND DAVID R. CARRIER*

Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT 84112-0840, USA

*e-mail: carrier@biology.utah.edu

Summary

The storage and recovery of elastic strain energy in muscles and tendons increases the economy of locomotion in running vertebrates. In this investigation, we compared the negative and positive external work produced at individual limb joints of running dogs to evaluate which muscle–tendon systems contribute to elastic storage and to determine the extent to which the external work of locomotion is produced by muscles that shorten actively rather than by muscles that function as springs. We found that the negative and positive external work of the extensor muscles is not allocated equally among the different joints and limbs. During both trotting and galloping, the vast majority of the negative work was produced by the two distal joints, the wrist and ankle. The forelimb produced most of the negative work in both the trot and the gallop. The hindlimb produced most of the positive work during galloping, but not during trotting. With regards to elastic storage, our results indicate that the forelimb of dogs displays a greater potential for storage and recovery of elastic energy than does the hindlimb. Elastic storage appears to be more important during trotting than during galloping, and elastic storage appears to be more pronounced in the extensor muscles of the distal joints than in the extensor muscles of the proximal joints. Furthermore, our analysis indicates that a significant portion of the external work of locomotion, 26 % during trotting and 56 % during galloping, is produced by actively shortening muscles. We conclude that, although elastic storage of energy is extremely important to the economy of running gaits, actively shortening muscles do make an important contribution to the work of locomotion.

Key words: locomotion, muscle, work of locomotion, locomotor energetics, dog, galloping, trotting.

Introduction

Elastic storage of energy in the muscles and tendons of running vertebrates has been shown to play an important role in the economy of locomotion (Cavagna *et al.* 1964; Alexander and Vernon, 1975; Heglund *et al.* 1982*b*; Taylor, 1994; Roberts *et al.* 1997) and appears to be pervasive in species specialized for running (Alexander, 1988; Full, 1989). Alexander (1984) provided an analysis of possible sites where elastic energy could be stored in the limbs of large mammals. He concluded that the majority of the energy is stored in the tendons located distal to the knee and elbow. In a hopping kangaroo, these strain energy stores accounted for 20–36 % of the total energy required to hop (Alexander and Vernon, 1975).

Recently, a general model for locomotor mechanics, the spring-mass model, has been employed to describe running mammals (Blickhan, 1989; McMahon and Cheng, 1990; Alexander, 1992; Full and Blickhan, 1992; Farley *et al.* 1993). These studies have shown that whole-body mechanics and kinematics of running mammals can be described by a simple model consisting of a point mass bouncing along on a single spring. The success of the spring-mass model and comparative analyses of the energetics of running (Taylor, 1994) have led many physiologists to adopt a working hypothesis of running

animals as systems in which elastic storage is the primary mechanism for the production of work. Implicit in this hypothesis is the assumption that muscles that do not behave as springs, but rather produce work by active shortening, do not make a significant contribution to the mechanics and energetics of running. This hypothesis of running appears to be in conflict with Alexander's (1984) studies in which he suggested that elastic storage occurs primarily in the joints distal to the knee of large mammals and may account for less than 50 % of the total energy required for running.

Another reason to suspect that terrestrial mammals may not be ideal spring-mass systems is that they do more than simply run at a constant speed on a level surface. For many species, energetically efficient locomotion is probably less important to survival and fitness than is an ability to accelerate and decelerate rapidly. Additionally, animals must maneuver in variable terrain which requires running up and down hill. Rapid accelerations require muscles that shorten actively to produce work (Cavagna *et al.* 1971) as does running up hill (Roberts *et al.* 1997). Shortening muscles in series with elastic elements could be expected to expend energy in stretching the elastic elements, thereby dissipating the displacement applied

to the center of mass and reducing the acceleration of the animal. Consequently, one might expect the limbs of running mammals to be a composite of muscle–tendon systems that have a pronounced capacity for elastic storage and other muscle–tendon systems that are designed to produce work by active shortening.

This study attempts to distinguish muscle–tendon systems that act as springs from those that actively shorten to produce work in running dogs. To do this, we used an analysis of the external work of locomotion at a number of limb joints during trotting and galloping. By analyzing the negative and positive work on a joint-by-joint basis, and by making measurements of length changes in two primary extensor muscles, we present a more complete description of which muscle–tendon systems are set up to behave as springs and the proportion of the external work of locomotion that may be accomplished by elastic storage.

Materials and methods
Ground forces and joint kinematics

Single-limb ground reaction forces and joint kinematics were measured in three dogs during trotting and fast galloping, as described previously (Carrier *et al.* 1998). The dogs were the same individuals and ran at the same speeds as in the previous study (Carrier *et al.* 1998, Table 1). The subjects ran down a carpeted track-way, 50 m long, with a force plate (Kistler, 9281B SN; 0.4 m×0.6 m) located mid-track and mounted flush with the track floor. Only trials in which a dog ran at relatively constant speed over the force plate were analyzed. Ground forces were sampled at 1000 Hz with an analog-to-digital acquisition and analysis system (BioPac Systems, Inc.) and stored on a Macintosh computer. The

positions of the limb joints were monitored using video at 120 images s^{-1} (Peak Performance Inc.) as the dog moved over the force plate.

We must acknowledge that our ability to locate the position of the shoulder (scapulo-humeral) joint in the video recordings of the force plate trials was very limited. The scapulae and humerus move through large displacements during the course of limb support, and the bones are surrounded by large muscles. These factors made it very difficult to determine the location of the shoulder joint in the video recordings. To provide a more accurate assessment of the change in angle of the shoulder joint during limb support than could be obtained from our video recordings, we analyzed cineradiographic recordings of three other dogs running on a treadmill (Carrier *et al.* 1998). Consequently, our calculations of the external work done at the shoulder joint are dependent on kinematic data from the force plate recordings, which may contain significant errors, and from measurements of changes in joint angle that came from a different set of dogs.

External work

To investigate which limb joints have the potential to store and recover elastic energy, we compared the negative and positive external work produced or absorbed by the extensor muscles at the six major limb joints (wrist, elbow, shoulder, ankle, knee and hip) during limb support. Work (*W*) produced by the muscle–tendon systems at each joint during a given time interval can be calculated by the following equation (Fig. 1):

$$W = |\overline{\mathbf{F_g}}|(\overline{R}\mathrm{d}\beta), \tag{1}$$

where $|\overline{\mathbf{F_g}}|$ is the mean magnitude of the resultant ground reaction force in one 8.3 ms interval [$=0.5(|\mathbf{F_{g2}}|+|\mathbf{F_{g1}}|)$], $\overline{R}$ is the
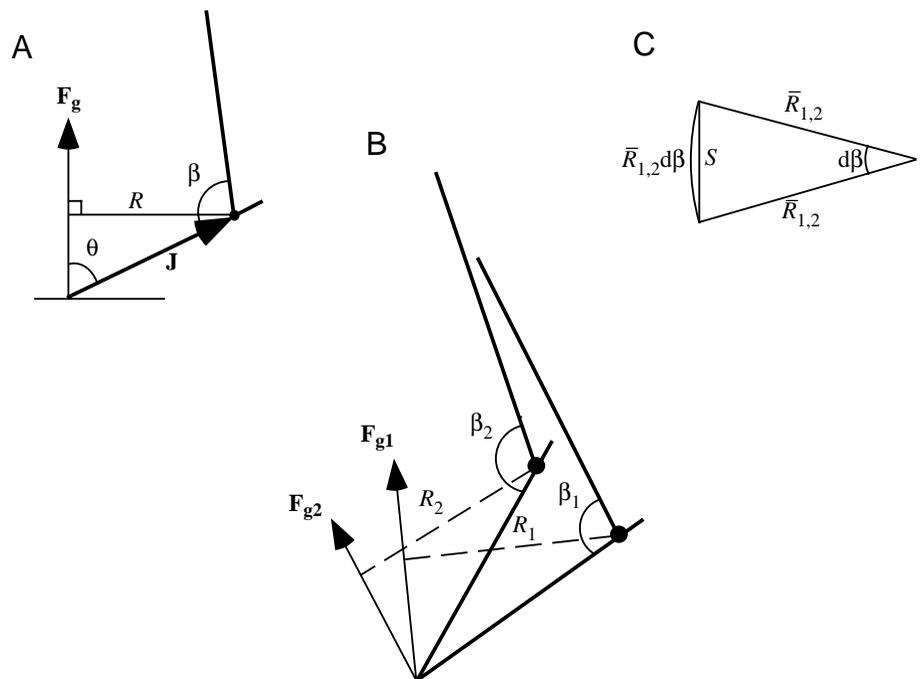
Fig. 1. Illustration of the method used to calculate external work. (A) Free body diagram of the foot showing how the effective ground force moment arm (*R*) was calculated. The ground reaction force (**F$_g$**), joint vector (**J**), joint angle (β) and the angle between the ground reaction force and the joint vector (θ) are labeled. (B) Free body diagram of the foot at two points in time during joint extension. (C) Schematic representation of the calculation of work. $\overline{R}_{1,2}$ is the mean ground reaction force moment arm between two 8.3 ms time intervals. $\overline{R}_{1,2}\mathrm{d}\beta$ is the arc distance covered by the effective moment arm. *S* is the linear displacement of the effective moment arm.

mean effective moment arm length over one 8.3 ms interval [=0.5(R_1+R_2)], and dβ is the angular displacement (in rad) of the joint during this time interval.

The ground reaction force was determined from the force plate recordings, where the origin of the ground reaction force is located at the center of pressure of the dog's foot. dβ, the angular displacement of the joint, was measured from the high-speed video at 8.3 ms intervals. *R*, the orthogonal distance from the vector of the ground reaction force to the axis of rotation of each joint, was computed as follows (Fig. 1A). The ground reaction force vector ($\mathbf{F_g}$) and joint vector ($\mathbf{J}$), defined as the distance and direction between the center of pressure and the joint, were crossed to yield the angle (θ) between them. The magnitude of the joint vector ($|\mathbf{J}|$) was then used as the hypotenuse of a right-angled triangle to calculate the moment arm *R* from the equation (Carrier *et al.* 1998):

$$R = |\mathbf{J}|\sin\theta. \qquad (2)$$

Although the work calculation described above yields the work produced or absorbed by a particular joint system, to compare our results with the work of previous authors (Cavagna *et al.* 1977; Heglund *et al.* 1982*a*; Full, 1989), we modified the calculation slightly to yield the work done by the joint systems on the center of mass of the animal. Because $\bar{R}$dβ is the arc distance covered by the effective moment arm

(Fig. 1C), and not a linear distance, this measure overestimates the work done on the center of mass of the animal. Consequently, rather than using the above equation for work, we computed work as follows:

$$W = |\mathbf{\overline{F_g}}|S, \qquad (3)$$

where *S* is the linear displacement (in m) of the moment arm in the direction of $\mathbf{F_g}$ (Fig. 1C).

S is given by the law of cosines:

$$S = [2\bar{R}^2 - 2\bar{R}^2\cos(d\beta)]^{0.5}, \qquad (4)$$

where $\bar{R}$ and dβ are defined above.

This approach, however, produced only small differences (approximately 0.3 %; our unpublished observations) from the work calculated using the conventional method (equation 1).

By convention, the work done during joint flexion was defined as negative and that done during joint extension as positive. Because our calculation of work always yields a positive result, to follow this convention, we used the direction of the joint angular displacement from the video recordings to determine the sign of the work.

Incremental values of work done by the extensor muscles (positive moment arm) were then summed to yield the total negative and positive work done by each joint (Fig. 2). To calculate the net negative and positive work done by all three
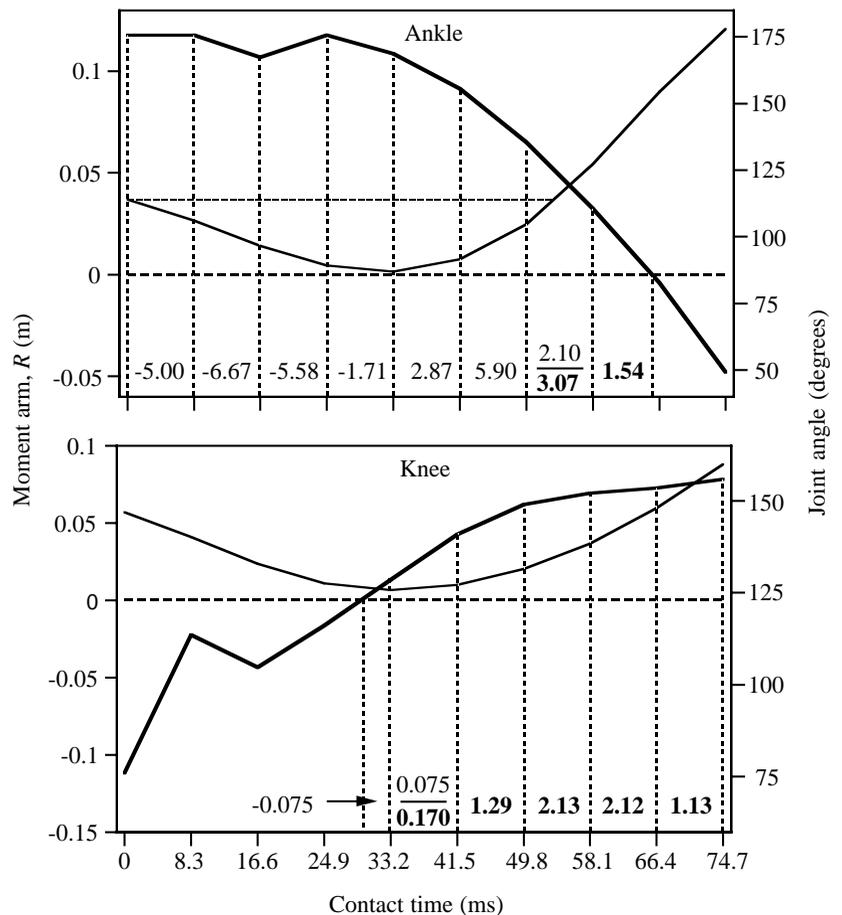
Fig. 2. Illustration of the method used to estimate the potential for elastic storage of energy. Data are shown for the ankle and knee joints from recordings of dog A galloping at 8.6 m s^{-1}. The traces begin (time 0) when the foot first touches the force plate and end when the foot lifts off the plate at 74.7 ms. Work (in J) was calculated at 8.3 ms intervals (dotted vertical lines) from the joint angular displacements (thin solid line), moment arms (bold solid line) and ground reaction forces (not shown). External work was calculated for the intervals in which there was an extensor moment (positive moment arm). These two plots show the major trends observed in all the joints analyzed. For the ankle, the joint angle at which spring rebound ends is illustrated with the fine horizontal dashed line. Work attributed to active muscle contractions is shown in bold print, while work attributed to elastic energy storage is shown in fine print.

joints in the fore- and hindlimbs, we summed the work done at each of the three joints in the limb at successive time intervals. For example, during the initial portion of hindlimb support, the knee and ankle joints flex to produce negative work while the hip joint extends simultaneously to produce positive work. At any time during support, the work produced by these three joints is the sum of their negative and positive contributions.

The work we calculated is the work done at each joint to accelerate and decelerate the center of mass of the dog (Biewener and Full, 1992) and is referred to as the external work of locomotion (Cavagna, 1975; Cavagna et al. 1977). The muscle–tendon systems of the joint must also perform work to accelerate and decelerate the limbs and to support the limb segments against gravity during the support phase. This 'internal work' was found to represent a small proportion (i.e. less than 10 % and usually less than 5 %) of the total work done during support in a preliminary inverse dynamic analysis which we performed on the data (our unpublished observations). Consequently, we are confident that our measures of external work provide an accurate assessment of the external work of locomotion. Values of external work are presented as means of the mean values from each dog. Standard deviations represent pooled values calculated from the total sample size. Sample size was 15 trials for trotting, 25 trials for forelimb galloping and 23 trials for hindlimb galloping (Carrier et al. 1998).

Potential for elastic storage

The calculations of positive and negative external work allowed the potential elastic storage of energy in the extensor muscle–tendon systems of each joint to be estimated (Fig. 2). To accomplish this measure of potential elastic storage, we adopted several assumptions or criteria. (1) The elastic elements are stretched during the period of limb support. It is possible that the elastic elements of some extensor muscles could be stretched during the deceleration portion of the swing phase of the limb. However, it seems unlikely that there could be much energy stored this way, especially considering the gracile nature of the limbs and the anatomy of the muscles that could potentially store elastic energy this way (Alexander, 1984). (2) If the elastic elements are stretched during the support phase, the joint in question would have to flex to stretch the spring and then extend to recover the stored energy during support. (3) Since a spring cannot recoil beyond the distance it has been stretched, the initial joint angle at the time of foot contact was considered to represent the resting length of the spring for that trial (Fig. 2). During joint extension, the spring was assumed no longer to have strain energy stored once the joint extended beyond the initial joint angle. Any positive work done by the extensor muscle–tendon system after the joint had extended beyond the initial joint angle was assumed to be due to active shortening of the muscle. (4) The extensor muscles must be active and exerting force during both flexion and extension of the joints. For calculations of work, we assumed that the extensor muscles were active and exerting force whenever the

moment was positive (i.e. an extensor moment). (5) The ground reaction force moment must be positive during both flexion and extension (Fig. 2). If the moment were negative (i.e. a flexor moment) during joint flexion, the elastic elements of the extensor muscles would not be stretched. If the moment became negative during joint extension, any energy stored in the extensor muscle–tendon systems during joint flexion would not be recovered.

Using the work calculations, we applied these criteria to calculate the potential for elastic storage at each joint. We assumed maximal energy storage and recovery when the mechanics fit the criteria (Fig. 2) so that all the energy put into the system as negative work would be recovered as positive work. The energy recovered was calculated as the proportion of positive external work that could be recovered from previously stored strain energy. Thus, our measure of elastic storage represents an estimate of the maximum that is theoretically possible on the basis of an analysis of the external work of locomotion. Therefore, it is likely that our analysis overestimates the amount of elastic strain energy stored and subsequently recovered by the six joints.

Shortening of the semimembranosus and long head of the triceps muscles

To evaluate further the potential for elastic storage at the hip and elbow joints, we measured the active shortening of the semimembranosus and the long head of the triceps muscles using sonomicrometry in four additional dogs as they trotted and galloped on a motorized treadmill (Table 1). For each muscle, we obtained a sample size of three dogs. The four dogs consisted of a small dalmatian (D in Table 1), a mongrel (E), a German shorthaired pointer (F), and a labrador retriever/basenji cross (G).

The methods used to measure muscle shortening are described in Carrier et al. (1998). The dogs were trained to trot and gallop comfortably on the treadmill prior to surgery. Two sets of cylindrical sonomicrometry transducers (CY 5-2, Triton Technology, Inc.) and associated electromyographic electrodes were surgically implanted into both muscles. The sonomicrometry transducers had previously been prepared by gluing each one to a steel mounting pin, which allowed the

Table 1. *Mass, running speeds and Froude numbers of the dogs used in the sonomicrometry recordings*

Dog	Mass (kg)	Trotting speed (m s⁻¹)	Froude number	Galloping speed (m s⁻¹)	Froude number
D	23	3.04	1.56	5.37	2.75
E	17	3.09	1.57	6.08	3.09
F	21	3.41	1.65	6.02	2.91
G	16	3.04	1.53	5.37	2.70

Froude number=$u/(gL)^{0.5}$, where u is forward velocity, g is the acceleration of gravity and L is the length of the hindlimb at mid-support (Farley et al. 1993).

transducer to be sutured in place on the muscle (Olson and Marsh, 1998). Each set of transducers was oriented along the length of the muscle fibers and positioned 12–18 mm apart. Implanted with each set of sonomicrometry transducers was an electromyographic electrode. These electrodes were of the sew-through type and were constructed and implanted as described previously (Betts *et al.* 1976; Carrier, 1996). Lead wires from the electrodes and transducers were fed subcutaneously to a dorsal exit point just caudal to the dorsal tips of the scapulae. Sonomicrometry and electromyographic signals were passed through shielded, lightweight cables (Cooner Wire Inc.) to the amplifiers. The sonomicrometry signals were processed with sonomicrometer modules (model 201; Triton Technology, Inc.), and the electromyographic signals were filtered above 1000 Hz and below 100 Hz, and amplified 5000–10 000 times using Grass P5 AC amplifiers. The signals were sampled at 2500 Hz with an analog-to-digital acquisition and analysis system (BioPac Systems, Inc.) and stored on a Macintosh computer.

Determination of the period in which active shortening of a muscle was measured was based on several criteria. First, we measured shortening of a muscle only during that portion of limb support in which the muscle moment was positive, as determined by Carrier *et al.* (1998). Active shortening that occurred during the swing phase or during portions of the support phase in which the muscle moment was negative were not included in our measurements. Second, we assumed a 20 ms delay from the initiation of the electromygram (EMG) signal and the generation of force by the muscle. Third, we assumed that active shortening of the muscle did not last for longer than 60 ms after the end of the EMG signal. We know of no measurements of the contractile properties of the semimembranosus or the long head of the triceps muscles in dogs that could be used to support our two assumptions of the relationship between the timing of the EMG signal and force generation by the muscle. We do, however, have simultaneous recordings of ground reaction forces and EMG activity from several hindlimb muscles of dogs performing vigorous jumps (our unpublished data) that are consistent with the timing relationships employed here.

Changes in the length of the muscles were calculated as a percentage of the length of the muscle when the subject was standing quietly (resting length). The fibers of the muscle were assumed to contract uniformly along the length of the muscle, and the change in distance between the transducers was divided by the distance between the transducers during standing. The percentage change in length was used to calculate the rate of shortening in muscle lengths per second. Means and standard deviations of percentage changes in length and the rate of shortening were calculated from a sample of 10 strides for each dog.

Mechanical linkage between the knee and ankle joints

To investigate whether mechanical energy could be transferred through the gastrocnemius and plantaris muscles from the knee to the ankle joint during the second half of the support period, we measured the extension of the ankle that results from extension of the knee. In a resting dog, the relaxed length of the two-joint gastrocnemius and plantaris muscles is such that extension of the knee joint produces extension of the ankle joint. Our measurements were made in three different dogs that had been killed (for an unrelated study) 1–3 h prior to our measurements. To measure angle changes, the skin was removed from one hindlimb of each dog. Small brass screws were driven into the mid-lateral shafts of the femur, tibia and fifth metatarsals, as well as into the axis of rotation of the knee and ankle joints. The fixed distances along the length of the bones between the screws in the shafts of the bones and the axis of rotation of the joint were measured. The limb was then held in a flexed position and the distance between the screws in the shafts of the femur and tibia and the distance between the screws in the shafts of the tibia and fifth metatarsal were measured. We then extended the knee joint a few degrees and repeated the measurements of the distances between the screws in the shafts of the bones. This was done through the full physiological range of knee extension. The law of cosines was used to calculate the angles of both joints at each of the settings. We then performed linear regressions of ankle angle on knee angle and normalized the results from each dog to allow the mean ankle angle for a given knee angle to be calculated.

Table 2. *Mean values of external work measured in three dogs during trotting and galloping including paired* t-*tests of positive* versus *negative work in each of the six joints*

	Trot				Gallop			
	Negative work ($J\,kg^{-1}\,km^{-1}$)	Positive work ($J\,kg^{-1}\,km^{-1}$)	d.f.	*P*-value	Negative work ($J\,kg^{-1}\,km^{-1}$)	Positive work ($J\,kg^{-1}\,km^{-1}$)	d.f.	*P*-value
Wrist	−187.9±54.8	112.7±52.5	14	<0.001	−164.1±85.5	88.4±35.2	24	<0.001
Elbow	−98.8±40.9	50.7±29.2	14	<0.005	−66.5±58.0	56.5±47.9	24	>0.10
Shoulder	−16.6±11.8	41.5±9.5	14	<0.0005	−26.0±15.9	38.1±14.1	24	<0.01
Ankle	−156.8±30.3	108.3±28.3	14	<0.001	−249.8±101.6	155.2±56.0	22	<0.0005
Knee	−23.8±14.6	38.5±14.4	14	<0.025	−4.1±5.0	78.6±42.6	22	<0.0005
Hip	0±0	48.3±19.8	14	<0.0005	0±0	144.3±61.8	22	<0.0005

Values are means ± S.D.

Table 3. *Mean values of external work in the fore- and hindlimbs measured as the summed values at successive time intervals in three dogs during trotting and galloping*

	Trot		Gallop	
	Negative work ($J\,kg^{-1}\,km^{-1}$)	Positive work ($J\,kg^{-1}\,km^{-1}$)	Negative work ($J\,kg^{-1}\,km^{-1}$)	Positive work ($J\,kg^{-1}\,km^{-1}$)
Forelimb	−290.3±56.1	191.1±70.6	−247.1±99.7	165.0±68.0
Hindlimb	−126.2±36.6	140.3±31.8	−142.5±62.6	272.3±81.7
Total × 2	−832.9±133.9	662.7±154.9	−779.3±235.4	874.7±212.6

Values are means ± S.D.

Results

External work of the extensor muscles

Mean values of negative and positive external work produced by the extensor muscles at each joint from three dogs during trotting and galloping are listed in Table 2. Each of the different joints contributed a greater or lesser extent to the negative and positive work. Generally, each joint produced a net negative or net positive amount of work. For example, the wrist and ankle joints produced more negative work than positive work during both the trot and gallop, whereas the shoulder and knee joints produced more positive work. The hip joint produced only positive work during both trotting and galloping.

The work produced at the three joints of the forelimb and three joints of the hindlimb can be summed at successive time intervals to yield the positive and negative work produced by the limbs (Table 3). The forelimb produced most of the negative work, generally approximately two-thirds of the total negative work produced by the six joints during both the trot and gallop. During galloping, the hindlimb produced most of the positive work (*P*<0.05, Student's *t*-test), approximately 62 % of the total. This was not true during trotting, when the forelimb produced more positive work (58 % of total) than did the hindlimb (*P*<0.05). If the work values for the fore and hindlimbs are multiplied by two to account for all four limbs, an estimate of the total work done on the center of mass by the six joints is obtained (Table 3). Note that this estimate

excludes the work done by the toe joints, the scapular-thoracic joint and the back. Summing the work for the six joints yields 833 $J\,kg^{-1}\,km^{-1}$ of negative work and 663 $J\,kg^{-1}\,km^{-1}$ of positive work during trotting and 779 $J\,kg^{-1}\,km^{-1}$ of negative work and 875 $J\,kg^{-1}\,km^{-1}$ of positive work during galloping.

In this analysis, the sample size did not allow us to address differences in the work produced by the joints of the leading and trailing limbs during galloping. Consequently, the values presented in Table 2 are composites of both leading and trailing limbs. The limited comparisons that we were able to make suggested that there were no differences in the work produced by the wrist, elbow, shoulder and ankle joints of the leading and trailing limbs. The hip joint of the leading limb, however, did appear to produce more positive work than the hip joint of the trailing limb, and the knee joint of the trailing limb may have produced somewhat more positive work than the knee joint of the leading limb. These differences, however, were not significant in our limited sample.

Positive work that can be attributed to the recovery of elastic energy

We calculated the positive work that could potentially result from the storage and recovery of elastic stain energy at each joint. This estimation was based on five criteria, as described in the Materials and methods section (Fig. 2). First, we compared the relative amounts of negative and positive work that occurred at a given joint during the period of stance in

Table 4. *Positive external work that could result from elastic storage (spring) and that which must result from actively shortening muscle (muscle), and the potential percentage recovery from elastic storage at each of the six joints*

	Trot			Gallop		
	Spring ($J\,kg^{-1}\,km^{-1}$)	Muscle ($J\,kg^{-1}\,km^{-1}$)	Recovery (%)	Spring ($J\,kg^{-1}\,km^{-1}$)	Muscle ($J\,kg^{-1}\,km^{-1}$)	Recovery (%)
Wrist	106.7±50.1	6.0±4.7	95.7±3.7	63.6±25.3	24.6±37.3	81.1±23.2
Elbow	48.3±29.4	2.4±3.3	96.1±5.7	30.1±34.3	26.4±41.1	58.7±38.9
Shoulder	16.6±11.7	24.9±9.9	37.7±20.9	21.1±12.9	17.0±10.5	48.7±24.3
Ankle	104.9±26.8	3.3±2.2	96.9±1.8	128.5±55.9	22.5±24.3	84.7±19.8
Knee	19.6±10.1	16.8±9.5	60.2±19.3	4.1±5.0	74.6±39.4	4.7±4.6
Hip	0±0	48.3±19.8	0±0	0±0	144.3±61.8	0±0
Total	296.1	101.7	74.4	247.4	309.4	44.4

Values are means ± S.D.

which the extensor muscles had a positive moment. If no negative work occurred at a given joint during this period, no energy could have been stored in the elastic elements of the joint's extensor muscle and tendons. Second, we assumed that the extensor elastic elements could rebound only to the extent they had been stretched during the negative work portion of stance. Thus, if more extension than flexion occurred at a joint, we assumed that extension beyond the total amount of flexion could not have resulted from recoil of elastic elements.

Our estimation of the potential for elastic storage indicates that the extensor muscle–tendon systems of the wrist and ankle joints can function as effective springs during both trotting and galloping (Table 4). During trotting, up to 97 % of the positive work done by these two joints could have resulted from the recovery of elastic energy that had been stored during the first half of the limb support period. During galloping, the potential for elastic storage at the wrist and ankle joints was only slightly less, 81 and 85 % recovery, respectively. The elbow joint also had the potential to store and recover elastic energy, but exhibited a bigger difference between trotting and galloping. Although there was potential for over 96 % recovery at the elbow joints during trotting, less than 60 % of the positive work could have resulted from elastic storage during galloping. The shoulder exhibited the opposite pattern; a 49 % potential to store and recover elastic strain energy during galloping, but only a 38 % potential for elastic storage during trotting. Approximately 60 % of the positive work produced by the knee joint could have resulted from elastic storage during trotting, but less than 5 % could have been recovered during galloping. Finally, because no negative work occurred at the hip joint, our analysis suggests that none of the positive external work produced by the extensor muscles of the hip joint resulted from elastic storage.

An estimate of the total positive external work from the six joints that could be due to elastic storage can be obtained by summing the 'spring' positive external work in Table 4. This indicates that as much as 74 % during trotting, and 44 % during galloping, of the external positive work done at the six joints could have been due to recovered elastic strain energy. Consequently, at least 26 % and 56 % of the positive external work during trotting and galloping, respectively, appears to have been supplied by muscles that actively shorten.

Shortening of the semimembranosus and long head of the triceps muscles

The semimembranosus muscle exhibited two patterns of shortening during the support phase of the locomotor cycle in both trotting and galloping dogs (Fig. 3). During trotting in two of the three dogs, the semimembranosus muscle displayed EMG activity but no appreciable length change shortly before the beginning of the support phase and during the first 15–20 % of the support period (Fig. 3A). The muscle then shortened at a roughly constant rate throughout the rest of the limb support period. However, only the initial portion of this shortening was considered to be active shortening because the vector of the ground reaction force passes behind the hip at 40 % of the support phase (Carrier *et al.* 1998), indicating that the
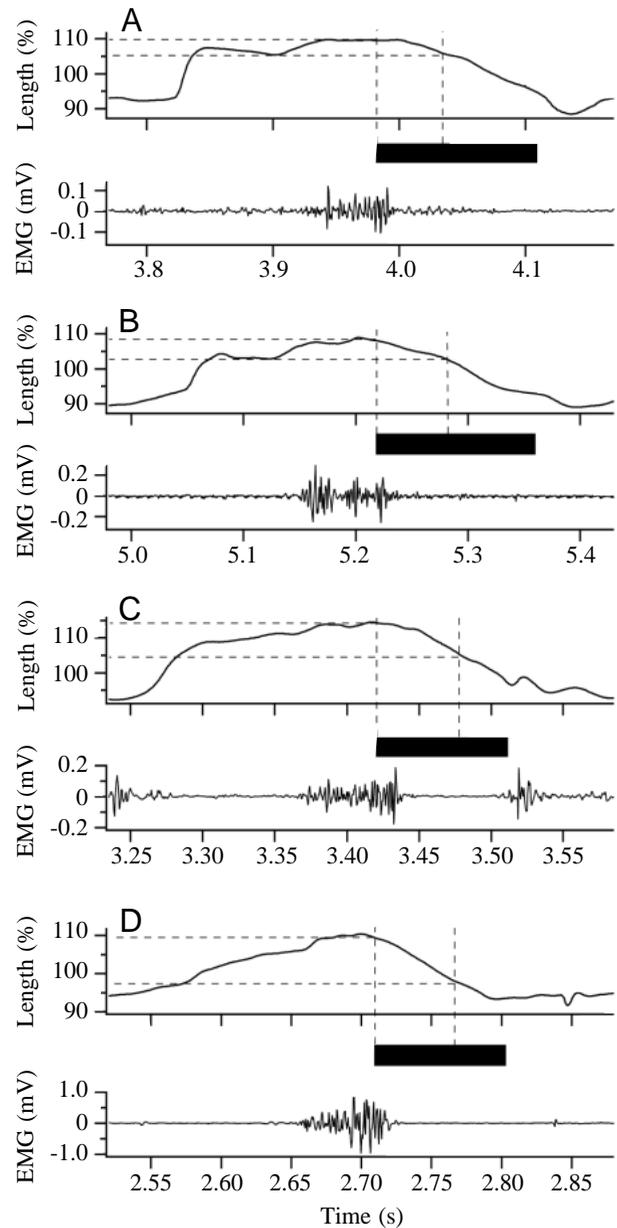
Fig. 3. Sample sonomicrometry and electromyography (EMG) recordings from the semimembranosus muscle from two dogs during trotting (A is for dog F and B is for dog G) and during galloping (C is for dog F and D is for dog G). In each case, the upper graph shows the changes in length of the muscle as a percentage of the resting length (length during standing) of the muscle. The lower graph shows the EMG activity. The filled bar denotes the duration of limb support. The vertical dashed lines indicate the period during which changes in muscle length and velocity were measured (see Materials and methods).

semimembranosus (and the other hamstring muscles) were no longer exerting force on the ground. The third dog displayed a pattern of continuous shortening during the period of support in which the moment of the semimembranosus was positive (Fig. 3B). All three dogs exhibited an active shortening of approximately 4.5–6.6 % of the resting length of the muscle,

Table 5. *Length change and velocity of shortening of the semimembranosus and the long head of the triceps brachii muscles*

	Semimembranosus			Triceps brachii (long head)		
	Dog E	Dog F	Dog G	Dog D	Dog F	Dog G
Length change (%)						
Trot	6.63±0.82	4.49±0.51	5.20±0.80	13.47±0.77	17.34±2.28	14.33±0.44
Gallop	9.34±0.88	9.21±0.52	10.32±0.95	10.24±1.07	20.82±2.17	17.84±2.68
Shortening velocity (muscle lengths s^{-1})						
Trot	1.07±0.12	0.66±0.07	0.88±0.16	1.38±0.14	1.86±0.24	3.61±0.58
Gallop	1.89±0.20	1.62±0.13	1.80±0.15	3.18±0.27	2.51±0.36	4.66±0.68

Values are means ± S.D., $N=10$.

Length change values are expressed as a percentage of the length of the muscle during standing (resting length).

and shortening velocities of 0.66–1.07 muscle lengths s^{-1} (Table 5).

During galloping, the semimembranosus muscle displayed the two patterns described above for trotting. In one dog, the muscle exhibited a period of isometric contraction at the beginning of support followed by active shortening at a constant rate (Fig. 3C). In the other two dogs (Fig. 3D), the muscle shortened throughout the period in which the extensors of the hip exerted force on the ground (i.e. the first 60 % of the support phase; Carrier *et al.* 1998). All three dogs exhibited active shortening of approximately 9.2–10.3 % of the resting length of the muscle and shortening velocities of 1.6–1.9 muscle lengths s^{-1} (Table 5).

The pattern of length change of the long head of the triceps muscle was more complicated than that observed in the semimembranosus, but the triceps also displayed two patterns of shortening during both trotting and galloping (Fig. 4). During trotting and galloping, two of the dogs (D and F) exhibited a pattern of active shortening initially, followed by active lengthening, and then a second period of active shortening during the period in which the extensor muscles of the elbow exerted force against the ground (Fig. 4A,C). In these two dogs, the total active shortening distance was relatively large, 10–21 % of resting length, and the mean shortening velocity was as high as 3.2 muscle lengths s^{-1} (Table 5). The third dog displayed high rates of active shortening early in the support phase, but this was followed by a long period of active lengthening (Fig. 4B,D). The shortening in this dog (dog G in Table 5) was substantial, 14–17 % of resting length, and the shortening velocity was very high, 3.6–4.7 lengths s^{-1}.

Fig. 4. Sample sonomicrometry and electromyography (EMG) recordings of the long head of the triceps muscle from two dogs during trotting (A is for dog F and B is for dog G) and during galloping (C is for dog F and D is for dog G). The upper trace for each graph shows the muscle length changes as a percentage of resting length, while the lower trace is the EMG activity. The filled bar denotes the duration of limb support. The vertical dashed lines indicate the period during which changes in muscle length and velocity were measured (see Materials and methods).
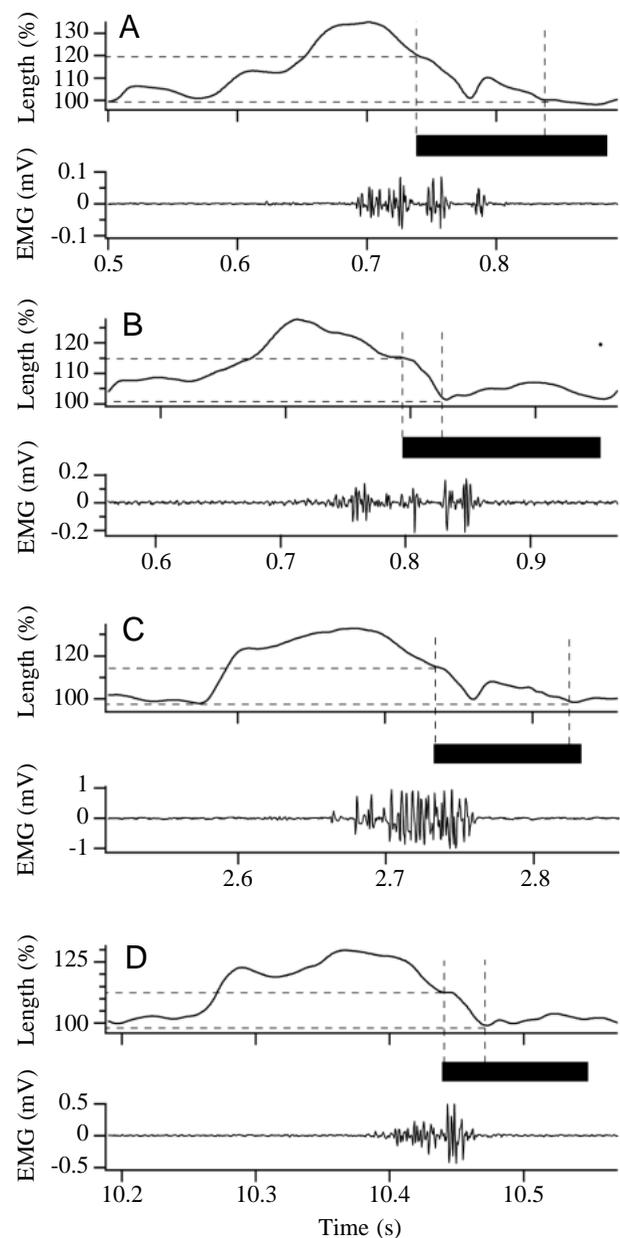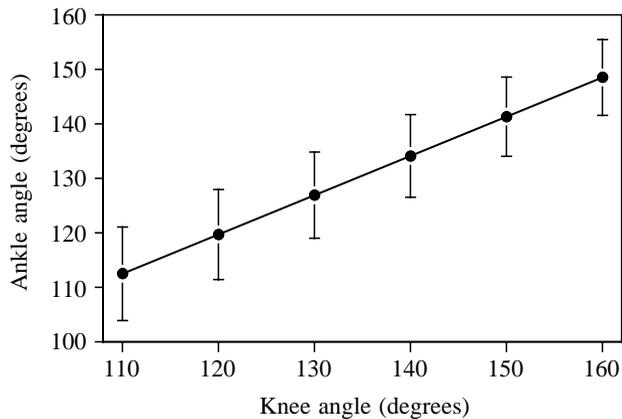
Fig. 5. Mean ankle angle plotted against knee angle as measured in three dogs. The error bars are the standard deviation. The line has a slope of 0.72.

Mechanical linkage between the knee and ankle joints

The gastrocnemius and plantaris muscles cross both the knee and ankle joints and have significant moment arms (r) at each joint. This results in a mechanical linkage in which extension of the knee joint produces extension of the ankle joint. A plot of the mean ankle angle *versus* knee angle for the three dogs produced a linear relationship with a slope of 0.72 (Fig. 5). Thus, when the gastrocnemius and plantaris muscles are relaxed, 1° of extension at the knee joint produces 0.72° of extension at the ankle joint. This relationship will also occur when the muscles are activated, but the corresponding angles at the two joints will change depending on the length of the muscles.

Discussion
Total external work

We have measured the mechanical work that six of the limb joints do on the center of mass of running dogs. Several previous studies measured the total mechanical work done during locomotion to lift and reaccelerate the center of mass (i.e. external work) in a variety of species, including dogs (Cavagna *et al.* 1977; Heglund *et al.* 1982*a*; Full, 1989). These studies used recordings of the forces applied to the ground over complete locomotor cycles to calculate changes in the instantaneous kinetic and potential energies of the center of mass. It is instructive to compare our value of the summed external work of the six joints of the dogs with the results of these previous studies. It must be kept in mind, however, that our estimate of 'total' external work is incomplete. The summed work of the six joints addressed in this study does not include the external work that is produced by the back, the scapular-thoracic joint and the toe joints. Consequently, our summed values are not measures of the total mechanical external work.

Given this caveat, the summed mechanical external work done by the six limb joints is remarkably close to reported values of the total external work. Measurements of the total

energy changes of the center of mass show that dogs require 480–920 J kg^{-1} km^{-1} to trot at 3 m s^{-1} and approximately 900 J kg^{-1} km^{-1} to gallop at 8 m s^{-1} (Cavagna *et al.* 1977). Summing the positive work measured at each joint in our dogs, and multiplying this value by two to account for the four limbs, we obtained average mass-specific total external work requirements of 663 J kg^{-1} km^{-1} during trotting at 3 m s^{-1} and 875 J kg^{-1} km^{-1} during galloping at approximately 8 m s^{-1} in dogs (Table 3). The fact that our values are slightly lower than measurements of the total external work of locomotion is not surprising given that our measurement does not include the work produced by the scapular-thoracic joint, the toe joints or the axial musculo-skeletal system. Nevertheless, the small difference between our measurements and those that use the total energy changes in the center of mass suggest that most of the work of locomotion of running dogs is produced by the six limb joints analyzed in this study.

External work of the different joints

The negative and positive work of the extensor muscles is not allocated equally among the different joints. In both trotting and galloping, the vast majority of the negative work is done by the two distal joints, the wrist and ankle. In fact, during galloping, 81 % of the total negative work is produced by these two joints and the ankle contributes 98 % of the total negative work of the hindlimb. However, some of the energy required to produce this large amount of negative work at the ankle joint is almost certainly a result of energy transfer between the ankle and knee joints through the two joint muscles of the shank, as has been described in humans and cats (Prilutsky and Zatsiorsky, 1994; Prilutsky *et al.* 1996). Nevertheless, most of the energy absorption in a stride does occur at the distal joints, which are the joints that appear to be driven to the greatest extent by muscles that function as springs (see below).

This allocation of negative work to the distal joints is likely to reduce the cost of locomotion. The large amount of negative work at the wrist and ankle joints allows a relatively great amount of energy to be stored in the elastic elements of the muscle–tendon systems. Because muscles produce more force when they contract isometrically, the mass of a muscle can be reduced if most of the work it produces is through elastic storage. Minimizing the mass of the distal limb segments results in a disproportionate reduction in the internal work of locomotion (i.e. a decrease in the energy required to swing the limbs back and forth; Hildebrand, 1995). In another context, absorption of energy at the distal joints could also act to reduce the extent to which the more proximal (non-spring) muscles undergo large, potentially damaging, eccentric contractions (Katz, 1939; Faulkner *et al.* 1993). Thus, accomplishing most of the negative work of locomotion at the distal limb joints may improve the economy of running and minimize eccentric damage to more proximal muscles.

The knee joint does undergo flexion during the first half of support (Carrier *et al.* 1998) which, by convention, is considered to represent negative work. However, during most

of this period, the moment is positive for the flexor muscles of the knee (i.e. the hamstring and gastrocnemius muscles). The flexor muscles are working through the shank to push on the ground and accelerate the dog forward. Although the knee flexes during early support, it produces positive, rather than negative, work on the center of mass. This component of the positive external work was not addressed in our analysis.

The positive external work is allocated more evenly among the joints, with the extensor muscles of each of the six joints making a contribution. The extensor muscles of the hip joint make a significant contribution to the positive work, but produce no negative work in either the trot or the gallop. This is because the hip joint extends during the entire period of limb support (Carrier *et al.* 1998). The extensor muscles of the knee joint also produce much more positive than negative work. The magnitudes of the negative and positive work done at each joint are more similar during trotting than during galloping. This is relevant to the relatively greater capacity for elastic storage during trotting than during galloping (see below).

External work of the fore- and hindlimbs

The positive and negative work of running appears to be allocated differently between the fore- and hindlimbs. The forelimb produced most of the negative work in both the trot and the gallop. The forelimb also produced more positive work than the hindlimb when the dogs trotted. In contrast, during galloping, the hindlimb produced most of the positive work. Our observations underestimate the extent of this difference because they do not include the contribution of the back, which is thought to play a large role in the generation of positive work through the hindlimbs during galloping. The observation that there is a division of labor between the fore- and hindlimbs has been made previously (Cavagna *et al.* 1977; Jayes and Alexander, 1978; Heglund *et al.* 1982a). Generally, forelimbs have been found to make a greater contribution to deceleration (i.e. negative work), whereas hindlimbs contribute more to acceleration (i.e. positive work). Thus, our finding that the forelimbs produce more positive work than the hindlimbs during trotting ($P<0.05$) was unexpected. However, the forelimb can be expected to produce significant positive work during trotting without inducing major pitching of the body because the center of mass of dogs is located closer to the forelimbs than to the hindlimbs (the forelimbs support 64 % of the body weight during standing) and the forelimb applies acceleratory forces to the ground at approximately the same time as the contralateral hindlimb.

These conclusions are based on observations that do not include the work of the toe joints or the scapular-thoracic joint. Nevertheless, we believe that the patterns observed here will also hold for the whole limbs because most of the work produced by the limbs appears to result from the six joints addressed in this study.

Transfer of mechanical energy between the knee and ankle

The extensor muscles of the knee joint are probably responsible for more positive external work than our simple

measurements indicate. The two joint muscles of the shank have been shown to transfer mechanical energy from the knee joint to the ankle joint in cats and humans (Bobbert *et al.* 1986a,b; van Ingen-Schenau *et al.* 1990; Prilutsky and Zatsiorsky, 1994; Prilutsky *et al.* 1996) and this certainly occurs in dogs as well. Both the gastrocnemius and plantaris muscles originate on the caudal side of the distal end of the femur, and in dogs these muscles have a moment arm at the knee joint that is approximately 72 % as long as their moment arm around the ankle joint. Consequently, extension of the knee puts tension in these muscles and acts to extend the ankle. This is easy to observe by manipulation of the hindlimb in any relaxed dog. Thus, there are two mechanisms for extension of the ankle (1) shortening of the ankle extensor muscle–tendon systems (i.e. the gastrocnemius and plantaris muscles), and (2) extension of the knee produced by the quadriceps muscles.

The contribution that the extensor muscles of the knee joint make to the work of the ankle joint can be estimated from a consideration of the amount of ankle extension that is produced by the knee. Because shortening of the ankle extensor muscle–tendon systems acts in series with the extension of the ankle joint that occurs as a result of knee extension, their contributions to ankle extension are additive. During galloping, an average of 56 ° of extension occurs at the ankle and 38 ° of extension occurs at the knee, and the extension at these two joints occurs simultaneously (Carrier *et al.* 1998). Our observations from dissected limbs and manipulations of intact limbs indicate that there is a 1:0.72 relationship between the angular extension at the knee and the resulting extension of the ankle joint. Thus, if 27 ° (72 % of 38 °) of the 56 ° of extension that occurs at the ankle is due to knee extension, then 49 % of the total ankle extension is produced by shortening of the quadriceps muscles rather than by the extensor muscles of the shank. If we assume that the extension of the ankle due to extension of the knee occurs simultaneously with the extension of the ankle that results from shortening of ankle muscle–tendon systems, then approximately 49 % of the positive external work done at the ankle during the gallop is a result of shortening of the knee extensor muscles and only 51 % of the ankle work can be attributed to the ankle extensor muscles.

The positive external work measured at the knee is 21 % of the total work done by the three joints of the hindlimb and 14 % of the work done by all six joints addressed in this study (Table 2). However, if 49 % of the work done at the ankle joint is actually produced by the extensor muscles of the knee, then the total contribution of the knee extensor muscles to the positive external work produced by the hindlimb would be roughly 41 % rather than 21 %. Additionally, this indicates that 27 % of the total positive external work produced by the six joints analyzed in this study is actually produced by the extensor muscles of the knee. If this is true, the knee joint makes a relatively large contribution to the work of locomotion.

The mechanism described above produces external work at the ankle joint by the transfer of energy from the extensor muscles of the knee to the extensor muscles of the ankle.

Transfer of energy has also been shown to act in the opposite direction during the first half of support. During deceleration, energy is transferred from the ankle extensor muscles to the knee extensor muscles (Prilutsky and Zatsiorsky, 1994). The extent to which this occurs in running dogs is difficult to estimate because two sets of muscles produce flexion at the knee during the first half of limb support, the gastrocnemius and plantaris muscles and the hamstring muscles. Nevertheless, some of the negative external work that we measured at the ankle joint is almost certainly done by the extensor muscles of the knee joint as a result of energy transfer from the ankle to the knee.

Critique of recordings of muscle length

Within individual dogs, the sonomicrometry recordings of changes in the length of the semimembranosus and triceps brachii muscles were very uniform. Among dogs, however, changes in muscle length were more variable than we anticipated (Figs 3, 4; Table 5). We believe that our recordings do accurately represent the length changes that occurred at the sites we sampled. The variability could, therefore, be a function of differences among individual dogs or among different sites within individual muscles. Given the wide variety of dog breeds (see above) used in this study, it is not unreasonable to suggest that the variation was a function of differences in style of running between breeds. However, it is also possible that, during running at intermediate speeds, different regions of these muscles experience different intensities of activation and different ranges of shortening. To investigate this possibility is beyond the scope of the present study since it would require the implantation of a number of transducer sets in individual muscles.

Potential for elastic storage at the limb joints

Wrist and ankle

Applying the criteria described in the Materials and methods section, our analysis of the external work indicates that, during trotting, as much as 97 % of the positive work of the extensor muscles of the wrist and ankle could result from the recovery of elastic strain energy that had been stored during the first half of limb support. This result is consistent with observations of a number of studies that have found the extensor muscle–tendon systems of the distal joints to function as effective springs (Alexander and Vernon, 1975; Alexander, 1984; Dimery and Alexander, 1985; Ker *et al.* 1987; Roberts *et al.* 1997).

Elbow

During trotting, the elbow joint also exhibited a potential to recover as much as 96 % of the positive work from elastic strain energy. However, less than 60 % of the positive work produced at this joint during galloping can be recovered from elastic strain energy.

Our recordings of length changes in the long head of the triceps muscle (one of the extensor muscles of the elbow) indicate that it does not behave as a spring in trotting or galloping. For a muscle to function effectively as a spring, one would expect very little change in the length of the muscle fibers during limb support (Alexander, 1984; Roberts *et al.* 1997). Early in support, as the elbow was flexing, the long head of the triceps actively shortened by as much as 10–20 % of its 'resting' length. It then underwent active lengthening for a variable portion of support and then actively shortened again. This surprising pattern is almost certainly a product of the fact that the long head is a biarticulate muscle crossing both the shoulder and the elbow. The observed shortening at the beginning of support, as the elbow joint flexes, makes sense only in the light of the fact that the shoulder joint undergoes flexion during this period. Nevertheless, these large changes in length are not compatible with the hypothesis that the long head of the triceps muscle functions to store energy elasticity. There are, however, other heads of the triceps muscle, such as the accessory and medial heads, that may function as springs.

Shoulder

The shoulder joint exhibited an intermediate potential to store and recover elastic strain energy (38 % during trotting and 49 % during galloping). However, as mentioned in the Materials and methods section, our limited ability to measure accurately the position of the shoulder joint during the force plate recordings introduced significant uncertainty into the calculations of external work and thus to the potential for elastic storage for this joint. Consequently, these values represent our best estimate of variables that are very difficult to measure.

Knee

Our analysis of the positive and negative work indicates that the extensor muscles of the knee joint have a capacity to store and recover approximately 60 % of the positive work done during trotting, but less than 5 % of the positive work during galloping. These results imply that, although significant elastic storage may occur at the knee joint during trotting, little or no elastic storage occurs at the knee joint during galloping. However, our recordings of the length changes in the vastus lateralis muscle are not completely consistent with this finding (Carrier *et al.* 1998).

During trotting, two of the three dogs for which Carrier *et al.* (1998) provide trotting data exhibited very little length change during knee flexion and during the first half of knee extension. In many cases, the muscle was basically isometric during the first half of joint extension. This suggests that in trotting dogs the work done at the knee joint during the first half of joint extension results from the recovery of stored elastic strain energy. The third dog, however, exhibited active shortening throughout joint extension and a total active shortening of approximately 20 % of resting length, which is not consistent with elastic storage at the knee during trotting.

We also observed variation in the pattern of shortening of the vastus lateralis muscle during galloping. During galloping, the vastus lateralis muscle showed a pattern of active lengthening during joint flexion and active shortening of

9–22 % of resting length during joint extension (Carrier *et al.* 1998). In two of the dogs, this shortening occurred throughout joint extension at a relatively constant rate of 3.7–4.0 muscle lengths s^{-1}. Active shortening of this magnitude suggests that there is no elastic storage at the knee joint during galloping. However, in the other two dogs, we observed a period of isometric muscle activity during mid-support. In these dogs, the vastus lateralis underwent active stretching during the first part of joint flexion, became isometric during mid-support and then underwent active shortening during the second half of joint extension. This suggests that some elastic storage did occur at the knee joint in these dogs during galloping.

Given that our analysis of external work indicates that elastic storage does not occur at the knee during galloping, how can the isometric contraction of the vastus lateralis muscle during mid-support be explained? We suspect that these dogs were able to store elastic strain energy as a result of the transfer of energy from the ankle to the knee during the period of joint flexion, as discussed above. During flexion of the ankle joint, the active gastrocnemius and plantaris muscles exert a flexor moment on the knee joint which is probably to necessitate a balancing moment from the quadriceps muscles as the knee joint undergoes flexion. Thus, the aponeurosis of the vastus lateralis muscle could be stretched during knee flexion even though the joint is exerting a flexor moment on the ground. This transfer of energy from the ankle to the knee is a potential mechanism for elastic storage that our analysis of the external work cannot address. However, the fact that two of the dogs exhibited only continuous shortening of the vastus lateralis muscle and that the other two dogs displayed isometric contractions only during the first half of knee extension suggests that the contributions made by the knee joint to elastic storage are relatively minor during galloping.

Hip

Analysis of the external work indicates that the extensor muscles of the hip do not function as springs. Because the hip produces no negative work during limb support, there is no potential for energy to be stored as elastic strain energy. This observation has been made previously for the hip in hopping kangaroos (Alexander and Vernon, 1975; Alexander, 1984). In general, our sonomicrometry recordings from the semimembranosus muscle also indicate that the work of the hip is produced by actively shortening muscles. However, in two of the three dogs studied during trotting and in one of the three dogs during galloping, the semimembranosus muscle displayed a brief period of activity without shortening just before and just after the beginning of limb support. This period of isometric contraction is consistent with the possibility of the storage of elastic strain energy during the end of the swing phase of the limb, as the limb is decelerated by the activity of the hip extensor muscles such as the semimembranosus. Thus, there may be potential for elastic storage in the extensor muscles of the hip as a result of rapid deceleration of the limb during the end of the swing phase. We cannot, however,

directly evaluate this possibility using the analysis of the present investigation. Given that there are no tendons or aponeuroses associated with the semimembranosus, the elastic energy stored must be due to energy storage in the crossbridges of the muscle, which is not a very effective mechanism (Alexander, 1984).

Elastic storage: caveats and generalities

In this discussion, we have acknowledged two potential sources of energy for elastic storage that an analysis of external work cannot address. The first is the transfer of energy from distal to proximal joints through two-joint muscles such as the gastrocnemius (Prilutsky and Zatsiorsky, 1994). During the portion of limb support when the ankle joint undergoes flexion, force transmitted to the femur by the gastrocnemius and plantaris muscles acts to flex the knee joint. This flexor moment must be countered by the extensor muscles of the knee and could potentially be stored as strain energy in their series elastic components. The fact that two of our dogs exhibited continuous shortening of the vastus lateralis muscle during knee extension suggests that this means of elastic storage is not highly effective. The second source of energy that could be stored, but cannot be addressed in this study, is the energy used to decelerate the limb segments during the end of the swing phase. This could take place in the extensor muscles of the hip, and the observation of a brief period of isometric contraction in the semimembranosus muscle during the beginning of limb support suggests that some elastic storage does occur as the limb is decelerated during the end of swing. However, the fact that an isometric contraction occurs only briefly during the beginning of the period in which the semimembranosus exerts a moment on the ground and not at all in some dogs (Fig. 3) suggests that elastic storage does not make a play a large role in the work produced by the extensor muscles of the hip joint.

Recognizing the limitations of an evaluation of elastic storage based solely on an analysis of external work, we believe that a number of generalities regarding elastic storage can be drawn from this investigation. First, the forelimb of dogs displays a greater potential for the storage and recovery of elastic energy than does the hindlimb. All three forelimb joints exhibited a capacity for significant elastic storage, whereas only the ankle joint of the hindlimb appears to have potential for significant elastic storage in galloping gaits. Taking into consideration the transfer of energy from the knee to the ankle during the joint-extension phase of support, our calculations suggest that only 19 % of the positive work done by the three joints of the hindlimb during galloping could result from the recovery of elastic strain energy. In contrast, as much as 63 % of the positive work done by the three joints of the forelimb during galloping could result from elastic storage.

Another generality that is supported by this study is the suggestion that elastic storage may be more important in trotting gaits than in galloping gaits (Cavagna *et al.* 1977). Our

analysis indicates that, during trotting, elastic storage could account for as much as 74 % of the positive external work that occurs at the six joints. In contrast, during galloping, only 44 % of the positive work could possibly result from elastically stored strain energy. This observation is somewhat surprising given that the energy expended per unit distance is not very different between the two gaits (Taylor *et al.* 1982). One should remember, however, that there are other possible sites of energy storage during galloping that were not addressed in this study. During galloping, the large internal kinetic energy fluctuations associated with the parasagittal bending of the back can be stored in the large aponeurosis of the extensor muscles of the back (Alexander *et al.* 1985). Another energy-saving mechanism in the gallop is the exchange of gravitational and kinetic energy when the animal 'pole-vaults' on the two forelimbs. In a dog, this can amount to 15–30 % of the external work (Cavagna *et al.* 1977).

Finally, the extensor muscles of the distal joints appear to play a larger role in energy conservation through elastic storage than do the more proximal joints. Alexander (1984) made this observation previously, and our results show that the pattern of more elastic storage at the distal joints is more pronounced in the hindlimb than in the forelimb.

In summary, there appears to be greater elastic storage in the distal extensor muscles than in the proximal extensor muscles of the limb, greater elastic storage during trotting than during galloping, and greater elastic storage in the forelimb than in the hindlimb. These observations led us to conclude that not all the work of constant-speed running is accomplished through the storage and recovery of elastic strain energy. This analysis indicates that a significant portion of the external work of running, 26 % during trotting and 56 % during galloping, is produced by actively shortening muscles. Thus, although animals do bounce along like simple spring-mass systems when they run, and although the elastic storage of energy is extremely important to the economy of running gaits, actively shortening muscles do play an important role in producing the work of running.

References

ALEXANDER, R. McN. (1984). Elastic energy stores in running vertebrates. *Am. Zool.* **24**, 85–94.

ALEXANDER, R. McN. (1988). *Elastic Mechanisms in Animal Movement*. Cambridge: Cambridge University Press. pp. 30–50.

ALEXANDER, R. McN. (1992). A model of bipedal locomotion on compliant legs. *Phil. Trans. R. Soc. Lond. B* **338**, 189–198.

ALEXANDER, R. McN., DIMERY, N. J. AND KER, R. F. (1985). Elastic structures in the back and their role in galloping in some mammals. *J. Zool., Lond.* **207**, 467–482.

ALEXANDER, R. McN. AND VERNON, A. (1975). The mechanics of hopping by kangaroos (Macropodidae). *J. Zool., Lond.* **177**, 265–303.

BETTS, B., SMITH, J. L., EDGERTON, V. R. AND COLLATOS, T. C. (1976). Telemetered EMG of fast and slow muscles of the cat. *Brain Res.* **117**, 529–533.

BIEWENER, A. A. AND FULL, R. J. (1992). Force platform and kinematic analysis. In *Biomechanics, Structures and Systems: A Practical Approach* (ed. A. A. Biewener), pp. 45–73. Oxford: Oxford University Press.

BLICKHAN, R. (1989). The spring-mass model for running and hopping. *J. Biomech.* **22**, 1217–1227.

BOBBERT, M. F., HUIJING, P. A. AND VAN INGEN SCHENAU, G. J. (1986*a*). A model of the human triceps surae muscle–tendon complex applied to jumping. *J. Biomech.* **19**, 887–898.

BOBBERT, M. F., HUIJING, P. A. AND VAN INGEN SCHENAU, G. J. (1986*b*). An estimation of power output and work done by the human triceps surae muscle–tendon complex in jumping. *J. Biomech.* **19**, 899–906.

CARRIER, D. R. (1996). Function of the intercostal muscles in trotting dogs: ventilation or locomotion? *J. exp. Biol.* **199**, 1455–1465.

CARRIER, D. R., GREGERSEN, C. S. AND SILVERTON, N. A. (1998). Dynamic gearing in running dogs. *J. exp. Biol.* **201**, 3185–3195.

CAVAGNA, G. A. (1975). Force platforms as ergometers. *J. appl. Physiol.* **39**, 174–179.

CAVAGNA, G. A., HEGLUND, N. C. AND TAYLOR, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.

CAVAGNA, G. A., KOMAREK, L. AND MAZZOLENI, S. (1971). The mechanics of sprint running. *J. Physiol., Lond.* **217**, 709–721.

CAVAGNA, G. A., SAIBENE, F. P. AND MARGARIA, R. (1964). Mechanical work in running. *J. appl. Physiol.* **19**, 249–256.

DIMERY, N. J. AND ALEXANDER, R. McN. (1985). Elastic properties of the hind foot of the donkey, *Equus asinus*. *J. Zool., Lond.* **207**, 9–20.

FARLEY, C. T., GLASHEEN, J. AND McMAHON, T. A. (1993). Running springs: speed and animal size. *J. exp. Biol.* **185**, 71–86.

FAULKNER, J. A., BROOKS, S. V. AND OPITECK, J. A. (1993). Injury to skeletal muscle fibers during contractions. Conditions of occurrence and prevention. *Physical Ther.* **73**, 911–921.

FULL, R. J. (1989). Mechanics and energetics of terrestrial locomotion: bipeds to polypeds. In *Energy Transformations in Cells and Animals* (ed. W. Wieser and E. Gnainger), pp. 175–182. Stuttgart: Thieme.

FULL, R. J. AND BLICKHAN, R. (1992). Generality of spring-mass model in predicting the dynamics of many-legged, terrestrial locomotion. *Physiologist* **35**, 185A.

HEGLUND, N. C., CAVAGNA, N. C. AND TAYLOR, C. R. (1982*a*). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the center of mass as a function of speed and body size in birds and mammals. *J. exp. Biol.* **79**, 41–56.

HEGLUND, N. C., FEDAK, M. A., TAYLOR, C. R. AND CAVAGNA, G. A. (1982*b*). Energetics and mechanics of terrestrial locomotion. IV.

Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**, 57–66.

Hildebrand, M. (1995). *Analysis of Vertebrate Structure*. New York: John Wiley & Sons, Inc. 447pp.

Jayes, A. S. and Alexander, R. McN. (1978). Mechanics of locomotion of dogs (*Canis familiaris*) and sheep (*Ovis aries*). *J. Zool., Lond.* **185**, 289–308.

Katz, B. (1939). The relation between force and speed in muscular contraction. *J. Physiol., Lond.* **96**, 45–64.

Ker, R. F., Bennett, M. B., Bibby, S. R., Kester, R. C. and Alexander, R. McN. (1987). The spring in the arch of the human foot. *Nature* **325**, 147–149.

McMahon, T. A. and Cheng, G. C. (1990). The mechanics of running: how does stiffness couple with speed? *J. Biomech.* **23**, 65–78.

Olson, J. M. and Marsh, R. L. (1998). Activation patterns and length changes in hindlimb muscles of the bullfrog (*Rana catesbeiana*) during jumping. *J. exp. Biol.* **201**, 2763–2777.

Prilutsky, B. I., Herzog, W. and Leonard, T. (1996). Transfer of mechanical energy between ankle and knee joints by gastrocnemius

and plantaris muscles during cat locomotion. *J. Biomech.* **29**, 391–403.

Prilutsky, B. I. and Zatsiorsky, V. M. (1994). Tendon action of two-joint muscles: transfer of mechanical energy between joints during jumping, landing and running. *J. Biomech.* **27**, 25–34.

Roberts, T. J., Marsh, R. L., Weyand, P. G. and Taylor, C. R. (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113–1115.

Taylor, C. R. (1994). Relating mechanics and energetics during exercise. *Adv. vet. Sci. comp. Med.* **38**A, 181–215.

Taylor, C. R., Heglund, N. C. and Maloiy, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**, 1–21.

van Ingen-Schenau, G. J., Bobbert, M. F. and van Soest, A. J. (1990). The unique action of bi-articular muscles in leg extensions. In *Multiple Muscle Systems, Biomechanics and Movement Organization* (ed. J. M. Winters and S. L. Y. Woo), pp. 639–652. New York: Springer.