

Gear ratios at the limb joints of jumping dogs

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Abstract

An increase in gear ratio of the limb extensor muscles during joint extension has been suggested to be a mechanism that facilitates optimal power production by skeletal muscles. The objectives of this study were to: (1) measure gear ratios at the wrist, elbow, shoulder, ankle, knee, and hip joints of jumping dogs, (2) compute the work performed by each of these joints, and (3) measure muscle shortening velocity for a joint exhibiting an increasing gear ratio during joint extension. The gear ratio out-lever was computed by dividing the ground reaction force (GRF) moment by the GRF, whereas the in-lever was directly measured as the perpendicular distance from the joint center to the line of action of the extensor muscle. In addition, changes in fascicle length were measured from the vastus lateralis muscle using sonomicrometry. Of the joints examined, only the gear ratios at the shoulder and knee joints increased during jumping in a manner that could facilitate peak power production of actively shortening muscles. The vastus lateralis was found to shorten at an average velocity of 3.20 muscle lengths per second. This is similar to estimates of shortening velocity that produce peak muscular power in mammals the size of dogs. Additionally, the knee extensors were found to produce a large proportion (26.6%) of the positive external work of the limbs. These observations suggest that dynamic gearing in jumping dogs may allow the extensor muscles of the knee joint to shorten in a way that maximizes their power production.

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1. Introduction

Dynamic gearing has been proposed as a mechanism to improve locomotor performance (Carrier et al., 1994, 1998). The concept is similar to the gearing that is provided by the transmission of an automobile, in which up-shifting of gears during acceleration improves performance. Similarly, if an animal were to rely on actively shortening muscles during accelerations, its performance could be enhanced if the gear ratios of extensor muscles increased throughout the accelerations. Because the force produced by muscle fibers declines in a hyperbolic fashion as shortening velocity increases, there exists an optimal shortening velocity at which power production is maximized (Hill, 1950). Hence, the total power produced by a muscle during acceleration would be maximized if the muscle fibers were to shorten continuously at their optimal velocity

(Rome and Lindstedt, 1997). The gear ratio of a muscle that shortens at a constant rate, however, must increase if the muscle is to contribute to acceleration of the animal. Specifically, the ratio of the ground force moment arm to muscle moment arm would have to increase (up-shift) as the joint extends. This mechanism would maintain the muscle fibers at their optimal velocity for power production as the animal accelerates.

One activity that relies heavily on muscular power production is jumping (Bennet-Clark, 1977; Aerts, 1998; Roberts and Marsh, 2003). Here we investigate dynamic gearing in jumping dogs. There were three study objectives. Our first objective was to calculate the gear ratios of the extensor muscles of the major limb joints to determine if any of these joints exhibit a pattern of increasing gear ratio during jumping. The second objective was to measure length changes for an extensor muscle of a joint that exhibited an increasing gear ratio pattern. Our third objective was to compute the contribution of the joints with an increasing gear ratio to the total external work produced during jumping.

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2. Methods

The dogs used in this study were trained to jump vertically to the top of an elevated platform. The three dogs used were of mixed breed, a Dalmatian (Dog E), a German Shorthaired Pointer mix (F), and a Labrador Retriever mix (G). Their average mass was 20 ± 3.6 kg. The height of the platform was adjusted to the height that elicited the maximum jumping performance for each dog (0.845 m for two of the dogs and 0.905 m for the third dog). The dogs jumped from a surface containing a force plate (Kistler, 9281B SN) configured to record single-limb ground forces. Seven single-limb force recordings were obtained for the left forelimb and left hindlimb of each dog (from one dog, 8 recordings for the hindlimb were obtained). The dogs were allowed to approach the force plate with one locomotor cycle before executing the jump. The ground forces were sampled at 1900 Hz (BioPac Systems, Inc.).

The positions of the limb joints were monitored with video at 120 images per second (Peak Performance Inc.). The joint centers of rotation were shaved and marked with a permanent marker. Joint center positions were manually digitized. The coordinate-time data of all digitized points were filtered using a fourth-order, zero-phase shift, Butterworth, low-pass filter with optimally determined cut-off frequencies (Jackson, 1979). The optimal filter parameter was calculated from the curve of each filter parameter plotted on the x -axis and the percent average residual at each filter plotted on the y -axis. The second derivative of this curve was found at each filter parameter and groups of three-second derivatives were sampled consecutively until a group fell beneath a defined prescribed limit. The smallest filter parameter in this group was considered to be the optimal.

2.1. Calculation of gear ratios

The gear ratio for a muscle was defined as the length of its out-lever, or ground reaction force (GRF) moment arm (R), divided by length of its in-lever, or muscle moment arm (r) (Fig. 1). Gear ratio was determined for the extensor muscles of the shoulder, elbow, wrist, hip, knee, and ankle joints for each dog (Carrier et al., 1998). The GRF moment arm was computed from a sagittal plane analytical model, while the muscle moment arm was measured directly from the dogs.

To compute the GRF moment arm, we assumed two-dimensional motion during jumping and that contribution from inertial forces and moments of the limb segments to the joint moments were zero. Consequently, the sagittal plane joint moment was equal to the cross product of the position vector to the center of pressure from the joint center with the GRF vector (Fig. 1). The GRF moment arm was calculated by dividing the

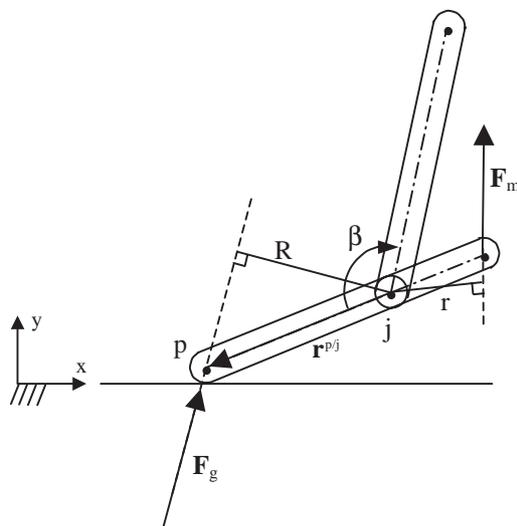


Fig. 1. Illustration of the method used to calculate gear ratio. For the generalized limb segment shown, R is the GRF moment arm, r is the muscle moment arm, F_g is the GRF vector, F_m is the muscle force vector, β is the joint angle, p is the center of pressure, j is the joint center, and $r^{p/j}$ is the position vector to the center of pressure from the joint center.

magnitude of the GRF joint moment by the magnitude of the single limb GRF. This distance is the perpendicular distance to the joint center from the line of action of the GRF (Fig. 1). By convention, a positive GRF moment indicated that the GRF acted to flex the joint, i.e. a net extensor moment, and a negative GRF moment indicated the reaction force acted to extend the joint, hence a net flexor moment (Winter, 1990). The gear ratio calculations utilized the same convention.

The muscle moment arm, r , was measured directly from each dog. The perpendicular distance from the joint's center of rotation to the line of applied force from the muscle was measured from each dog as it rested with the joint in flexed (90° for elbow and ankle) and fully extended positions. The center of rotation of the joint was visually identified by rotating the limb segments by hand. Handheld calipers were used to measure the distance between the joint center and the line of action of the tendon. Values of the muscle moment arm for intermediate joint angles were interpolated by assuming that the length of the moment arm changed in a linear manner from flexed to fully extended joint angles. A sensitivity analysis—performed using a linear assumption, a nonlinear assumption, and a constant value of r —verified that an assumption of a linear change in moment arm was appropriate.

For each jumping trial, the gear ratio values were interpolated to obtain values as a percentage of support in 10% increments. The same method was employed for the joint excursion curves. Average gear ratio and joint excursion curves were generated for each dog from these trials, which were then used to compute the average for the three dogs used in this study.

2.2. External work

External work (Cavagna, 1975; Cavagna et al., 1977) at each joint was computed using the GRF moment arms and force magnitudes. For each sampling interval, joint work was computed by multiplying the average length of R , change in joint angle, and average magnitude of the GRF (Biewener and Full, 1992). This method is equivalent to integrating the joint power curve (Winter, 1990). By convention, if the joint were flexing while the GRF moment was positive, then the work was negative. Conversely, if a joint was extending while the GRF moment was positive, then the work was positive. For each joint, the positive and negative work were summed separately, resulting in estimates of total positive and total negative work performed by each joint.

To determine the net positive and net negative work performed on the center of mass during a jump an interval-sum analysis was performed. During jumping, there are portions of support in which some joints may be performing positive work while others may be performing negative work. For example, during the initial portion of hindlimb support, as the knee and ankle joints flex and negative work is done, positive work is done as the hip joint extends. At any time during support, the work performed on the center of mass by these three joints is the sum of their negative and positive contributions. Consequently, the work done by all the joints in each limb at successive time intervals was summed to estimate the net external work performed on the center of mass. Lastly, it was assumed that the contribution of the contralateral limb was symmetric, hence the positive and negative work calculated for the fore and hindlimbs was multiplied by two to obtain an estimate of net positive and negative external work performed on the center of mass of the animal during a jump.

All work values were normalized to body mass and jump height, and are presented as the energy required to elevate 1 kg, 1 m. Because single limb forces were necessary for gear ratio and joint work calculations, jump height could not be determined from the force platform records. As an alternative, vertical take-off velocity of the center of mass was estimated from the video recordings by tracking the apex of the iliac crest. The vertical velocity of this point was then used to compute the jump height.

2.3. Energy transfer

Biarticular muscles allow energy transfer between nonadjacent limb segments (van Ingen-Schenau et al., 1990; Prilutsky and Zatsiorsky, 1994). Estimating this type of energy transfer requires calculating the forces in the biarticular muscle tendon systems as well as the displacements of the elastic and contractile elements

(van Ingen-Schenau et al., 1990; Prilutsky et al., 1996a, b). This information was not available in this study. Hence, the effects of energy transfer were ignored in all but one case, the biarticular, extensor muscle-tendon systems of the calf. As observed by Gregersen et al. (1998) there exists a fixed mechanical linkage between knee and ankle joints of dogs. 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. The maximum relaxed length of the muscles requires extension of the ankle whenever the knee is extended. As determined by Gregersen et al. (1998), over the passive range of joint motions, 1° of knee extension requires 0.72° of ankle extension, or conversely, 0.72° of ankle flexion produces 1° of flexion at the knee. Although there may be some eccentric lengthening of the muscle fibers during the first half of limb support as the ankle flexes, inelastic lengthening of the muscle is unlikely to occur during extension of the ankle and knee joints when positive work is produced. This linkage simplifies the estimation of energy transfer between these two joints.

When this linkage was considered, the external work values of the knee and ankle joints extensor muscles had to be modified. Note first that this analysis was only performed when the extensor moment for both joints was positive. This condition was met during the latter portions of knee flexion and remained until the ankle moment became negative near the end of hind limb support. Accordingly, when the ankle and knee joints were flexing while both extensor moments were positive, the negative work of the ankle was decreased, while the negative work of the knee was increased based on this rotational displacement ratio. Conversely, during ankle and knee joint extension, while the joint moments were positive, energy was transferred from the knee to the ankle. For each trial, the amount of ankle external work for each time interval that could be attributable to knee joint external work was calculated.

2.4. Length changes of vastus lateralis muscle

Sonomicrometry transducers and electromyography (EMG) electrodes were surgically implanted in the lateral aspect of the vastus lateralis muscles to allow recording of changes in fascicle length as described previously (Biewener et al., 1998; Carrier et al., 1998). Determination of the period in which active shortening of a muscle occurred was based on two criteria. First, fascicle shortening was measured only during the portion of limb support in which the GRF moment was positive. Second, it was assumed that active shortening of the muscle did not begin until 20 ms after EMG onset, or last for longer than 50 ms after the end of the EMG signal. Changes in length of the fascicle were calculated as a percentage of length of the fascicle

when the subject was standing quietly (resting length). The change in percent length was used to calculate the rate of shortening in fascicle lengths per second.

3. Results

3.1. Gear ratio and joint excursion

The gear ratios of the extensor muscles changed dramatically during jumping (Fig. 2). Four of the six

joints examined (wrist, elbow, ankle and hip) exhibited a decrease in extensor gear ratio during jumping. In the wrist and ankle joints, there was a positive and roughly constant gear ratio for approximately the first 70% of support, followed by a quick decline in gear ratio. At the elbow and hip joints, the gear ratio started positive and declined in a roughly linear fashion, becoming negative toward the end of support. The shoulder and knee joints displayed a different pattern. The gear ratios at these joints started out negative and increased linearly throughout the jump. The gear ratio became positive

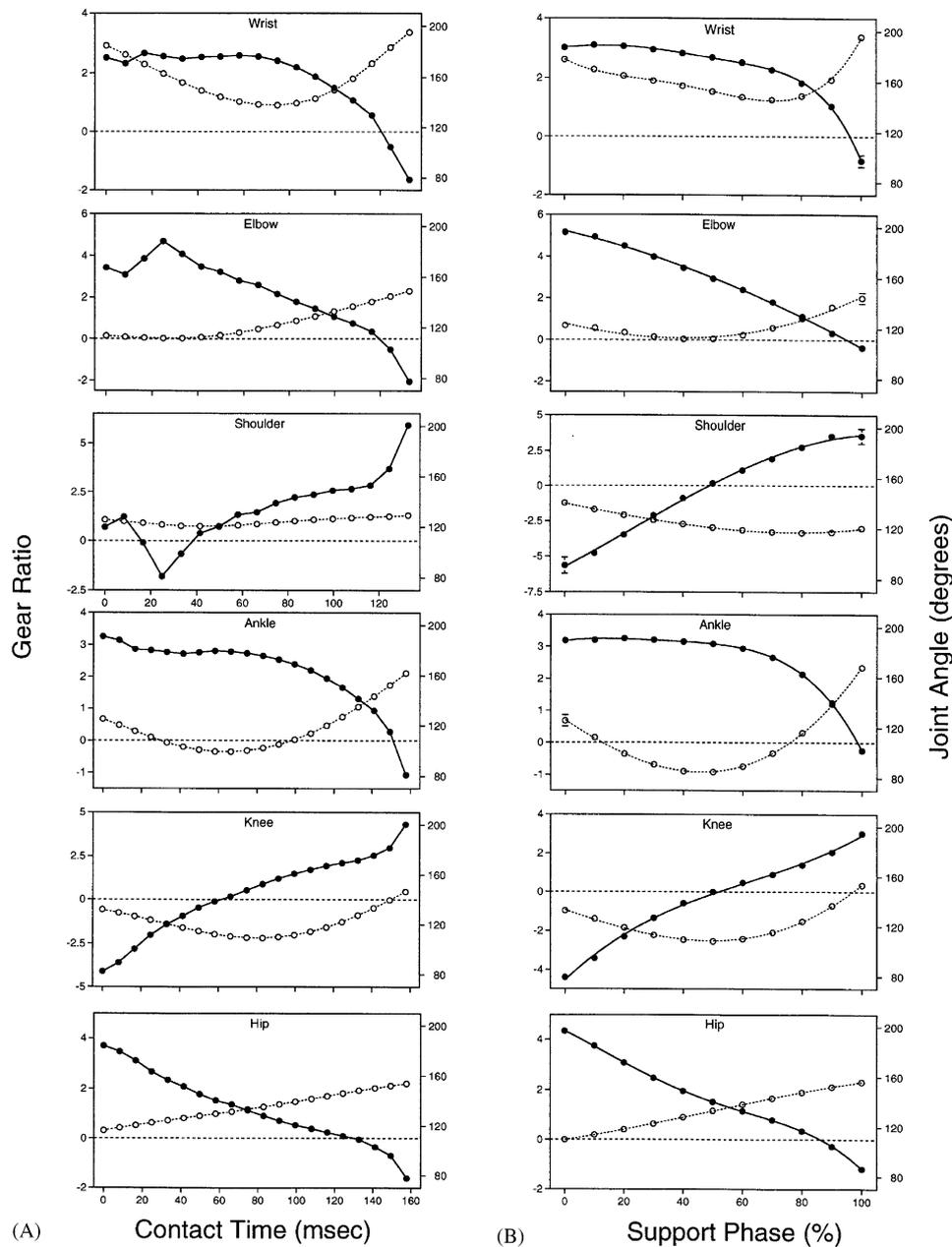


Fig. 2. Gear ratios of the extensor muscles (solid lines) and joint angles (dashed lines) plotted as a function of contact time (limb support) during maximum vertical jumps: (A) sample data from a jump by dog E; (B) means and standard errors of the data from three dogs plotted relative to support phase. Each point represents the mean of the mean values from each dog ($n = 7$ jumps). Standard errors were very small. Gear ratios greater than zero represent positive extensor muscle moments. Declining joint angles indicate flexion of a joint.

midway through support at both joints. Thus, the knee and shoulder joints exhibited a gearing pattern that could allow their extensor muscles to shorten isokinetically as the joint extended.

For all joints, the length changes of the extensor muscle moment arm played a relatively small role in the changing gear ratio compared to the length changes of the GRF moment arm. While the muscle moment arm was always positive, the GRF moment arms transitioned from either a negative or positive length to a length of the opposite sign during support. In addition, the length changes of the GRF moment arms were of much larger magnitude than the muscle moment arms. Thus, the changes in gear ratio were due almost entirely to changes in length of the GRF moment arm.

The hip joint was unique in that it displayed only joint extension during the jumps (Fig. 2). The angular excursions of the other five joints (wrist, elbow, shoulder, ankle, and knee) were similar in that the joints flexed early in support, then extended.

3.2. Length changes of the vastus lateralis muscle

During jumping, the portion of the vastus lateralis muscle that we monitored underwent considerable length changes in all three dogs (Fig. 3 and Table 1). The average shortening of this portion of the muscle ranged from 17% to 29.5% of standing length in the three dogs. Shortening velocity ranged from 2.7 to 3.9 muscle lengths per second.

Although all three dogs displayed considerable shortening of the vastus lateralis muscle, there was variability in the pattern of shortening. In dogs E and G, the muscle began to shorten just after the GRF vector began to exert a positive moment on the knee joint (Fig. 3). In these dogs, the muscle shortened at a high and roughly constant velocity during the entire period of knee extension. In contrast, Dog F displayed a prolonged period of limited length change during mid-support. This period of limited length change was followed by pronounced active shortening, averaging 17% of standing length (Table 1).

3.3. External work

For most of the joints, the extensor muscles produced either a net negative or net positive amount of work (Table 2). In the forelimb, the extensors of the wrist joint produced significantly more negative work than positive work, whereas the elbow extensors produced nearly twice as much positive as negative work. The shoulder extensors produced equal amounts of positive and negative work. In the hindlimb, the extensors of the ankle produced considerably more positive work than negative work. The knee extensors produced very little negative work and the hip extensors produced no

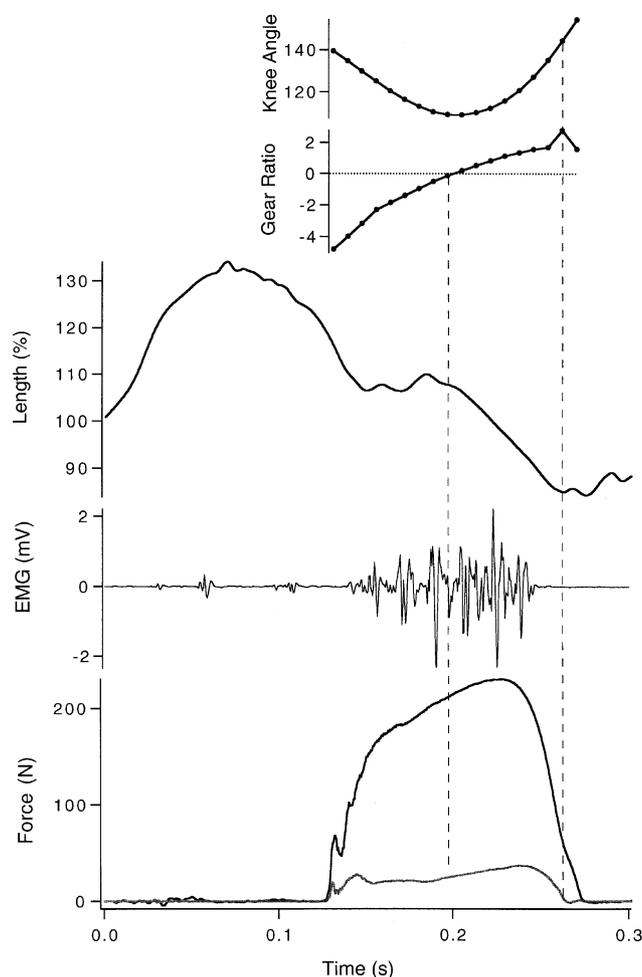


Fig. 3. Sample recordings of the length changes and EMG from the lateral aspect of the vastus lateralis muscle plotted relative to recordings of knee angle, gear ratio, and ground forces from dogs E jumping vertically.

Table 1
Shortening and velocity of the Vastus lateralis muscle in jumping dogs^a

	Dog E	Dog F	Dog G
Length change (%) ^b	26.0 ± 3.50	17.0 ± 0.583	29.5 ± 2.48
Shortening velocity (lengths per second)	3.86 ± 0.494	3.04 ± 0.177	2.71 ± 0.200

^a Mean ± 1 standard deviation ($n = 7$).

^b Length change expressed as a percentage of fascicle length during standing.

negative work, whereas both produced a significant amount of net positive work.

The forelimb produced 1.25 times more positive work than negative work, whereas the hindlimb produced 18.0 times more positive than negative work (Table 3). The positive work produced by the hindlimb was 4.5 times (80% of the total) more than that produced by the forelimb. Conversely, the negative work produced by the forelimb was more than 3.2 times that of the

Table 2

Mean and standard deviation of positive and negative external work measured at individual joints in three dogs during jumping

	<i>n</i>	Negative ($\text{J kg}^{-1} \text{m}^{-1}$)	<i>n</i>	Positive ($\text{J kg}^{-1} \text{m}^{-1}$)	<i>P</i> -Value ^a	% of limb ^b	% of total ^c
Wrist	21	-0.503 ± 0.149	13	0.344 ± 0.128	0.0027	31.7	7.1
Elbow	21	-0.359 ± 0.151	18	0.672 ± 0.170	0.0072	61.8	13.8
Shoulder	21	-0.114 ± 0.074	13	0.071 ± 0.066	0.2890	6.5	1.5
Ankle	9	-1.094 ± 0.255	22	1.759 ± 0.336	0.0040	46.7	36.3
Knee	22	-0.002 ± 0.003	22	0.560 ± 0.266	<0.0001	14.9	11.5
Hip	9	0 ± 0	9	1.446 ± 0.228	<0.0001	38.4	29.8

^a *P*-Value from *T*-test between negative and positive work.^b Values are percentages of the positive work of the limb.^c Values are percentages of the total positive work.

Table 3

Time interval-sum of positive and negative work of the fore and hindlimbs during jumping^a

	<i>n</i>	Negative ($\text{J kg}^{-1} \text{m}^{-1}$)	Positive ($\text{J kg}^{-1} \text{m}^{-1}$)
Forelimb	13	-0.525 ± 0.215	0.659 ± 0.183
Hindlimb	9	-0.164 ± 0.110	2.953 ± 0.295
Total times 2		-1.380 ± 0.484	7.224 ± 0.694

See methods for explanation

^a Mean \pm standard deviation

hindlimb. An estimate of the total external work done by the six joints was made by multiplying these interval sums of external work by two to account for all four limbs. This calculation yielded a total of $7.2 \text{ J kg}^{-1} \text{m}^{-1}$ of positive work and $1.4 \text{ J kg}^{-1} \text{m}^{-1}$ of negative work in an average jump. This estimate, however, did not include the work done by the back, the forelimb-thorax linkage, and the toe joints.

3.4. Mechanical linkage between the knee and ankle joints

When the linkage relationship of coupled rotation for the ankle and knee joints was applied to the external work measurements, the percentage of positive work for the ankle and knee joints shifted dramatically. The external work produced by the ankle was $1.76 \text{ J kg}^{-1} \text{m}^{-1}$, of which $0.73 \text{ J kg}^{-1} \text{m}^{-1}$ was due to the extension of the knee (Table 4). This represents 41% of the total positive external work done at the ankle. Only $1.03 \text{ J kg}^{-1} \text{m}^{-1}$ was actually produced by the extensor muscle of the ankle. Thus, including the work done at the ankle, the knee extensors produced 34% of the positive external work of the hind limb, and 26.6% of the total positive external work.

4. Discussion

4.1. Assumption of zero mass limb segments

The analytic model assumed that the mass and inertia of the limb segments were zero. Three observations

suggest that this assumption is justified. First, the mass and inertia contributions to joint moments have been shown to be small for jumping dogs (Alexander, 1974). Second, the mass and inertia contributions to joint moments have also been shown to be small for trotting goats (Pandy et al., 1988). Third, our results from a pilot study on dogs, using a sagittal plane inverse dynamics model (Winter, 1990), showed that during galloping the joint moments were affected, on average, by less than 5% for the hip and shoulder, with smaller differences calculated for the more distal joints (unpublished observations, Gregersen and Carrier).

4.2. Dynamic gearing

The drop in extensor muscle gear ratio observed at the wrist, elbow, and ankle joints could improve the potential for storage and recovery of elastic strain energy, in a manner similar to the mechanism that has been proposed for jumping frogs (Roberts and Marsh, 2003). The high gear ratios early in support could help stretch the elastic elements by applying large forces to the muscle-tendon systems. During this phase of joint flexion, the muscles would be near isometric or undergoing slight lengthening contractions, and because of the force-velocity relationship, and stretch-shortening relationship (Cavagna et al., 1986), the muscles could generate large forces. Then during joint extension, as the gear ratio declined, the force required from the muscle would diminish and the stretched elastic elements could recoil at high velocities, maximizing jumping power as has been suggested to be the case in frogs. In contrast, the drop in gear ratio that occurs at the hip joint is unlikely to facilitate storage and recovery of elastic strain energy because there is no joint flexion during limb support that would be necessary to stretch elastic elements.

Both the knee and shoulder joints exhibited a pattern of gearing consistent with the dynamic gearing hypothesis (Fig. 2). The gear ratios of these joints became positive just as the joints began to extend and the ratio increased in a roughly linear fashion throughout the period of joint extension. This pattern of increasing gear

Table 4

Positive extensor work of the ankle joint produced by the knee joint when the mechanical linkage between knee and ankle joints was incorporated

	Positive work (J kg ⁻¹ m ⁻¹)	Positive work w/linkage (J kg ⁻¹ m ⁻¹)	% of Hindlimb w/ linkage ^a	% of total ^b	% of ankle by knee
Ankle	1.759	1.029	27.3	21.2	41.5
Knee	0.560	1.289	34.3	26.6	
Hip	1.446	1.446	38.4	29.8	

^a Values are percentages of the positive work of the hindlimb when energy transfer is included in the calculation.^b Values are percentages of the total positive work of fore and hindlimbs when energy transfer is included in the calculation.

ratio could facilitate constant shortening velocity of the joints' extensor muscles, potentially at the velocity at which muscle power is maximized.

4.3. Length changes of the vastus lateralis muscle

The pattern of shortening of the vastus lateralis muscle (Fig. 3) was consistent with the hypothesis that dynamic gearing at the knee joint results in muscle shortening that is optimal for power production. The lateral aspect of the vastus lateralis muscle underwent substantial shortening (17–29% of standing length) at high rates (2.7–3.8 lengths per second) as the knee extended during jumping (Table 1). In two of the dogs, this shortening occurred at a relatively constant rate. However, the question remains as to whether or not the observed shortening could maximize muscle power.

We are not aware of any measurements of the contractile properties of the limb muscles of dogs; however, the shortening velocities measured here can be compared to estimates of peak shortening velocity from allometric relationships for the fast muscles of mammals (Close, 1972; Rome et al., 1990). The average shortening velocity of the vastus lateralis muscle of our jumping dogs was 3.20 muscle lengths per second. Assuming this portion of the vastus lateralis muscle shortened at a rate that produced peak power and that peak power occurred at 30% of V_{\max} (McMahon, 1984), then the data suggest that V_{\max} is approximately 10.7 muscle lengths per second (i.e., 3.2 m.l. s⁻¹ 0.30⁻¹). This prediction for V_{\max} of the vastus lateralis muscle is similar to estimates of V_{\max} from allometric equations of fast twitch muscle for a 20 kg mammal (10.0 fiber lengths per second (Close, 1972), and 12.5 fiber lengths per second (Rome et al., 1990)). Hence, the shortening velocities measured in this study appear consistent with the hypothesis that dynamic gearing allows the knee extensor muscles to shorten at a rate that maximizes their power production during jumping.

4.4. External work

If dynamic gearing were an important mechanism in achieving maximum jumping height for a dog, then we

would expect a large portion of the total work of a jump to be produced by the shoulder and knee joints. Our analysis of external work suggests that the extensor muscles of the shoulder joint produce an insignificant amount of positive external work (Table 2). However, when the transfer of energy from the knee to the ankle joint is considered, the extensor muscles of the knee joint produce 34% of the positive work of the hindlimb and 27% of the total positive work of the fore and hind limbs. It is important to keep in mind that these estimates of energy transfer do not include possible work done at the knee joint due to work done by the hip extensors and transferred to the knee by the two-joint rectus femoris (van Ingen-Schenau et al., 1990; Prilutsky and Zatsiorsky, 1994; Prilutsky et al., 1996a, b; Jacobs et al., 1996), or the possibility of energy generated by the knee extensors being transferred to produce hip extension via the two-joint hamstrings (Jacobs et al., 1996). Nevertheless, our estimate indicates that the knee joint extensor muscles are major contributors to the total work of a jump (Table 4). Thus, the large amount of work done by the extensors muscles of the knee, plus the observed pattern of shortening of the vastus lateralis muscle, suggest that dynamic gearing in jumping dogs may allow the extensor muscles of the knee joint to shorten in a way that maximizes their power production.

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