ELECTRICAL ACTIVITY AND RELATIVE LENGTH CHANGES OF DOG LIMB MUSCLES AS A FUNCTION OF SPEED AND GAIT

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SUMMARY

Electrical activity and length changes of 11 muscles of the fore- and hind-limbs of dogs walking, running, and galloping on a treadmill, were measured as a function of forward speed and gait. Our purpose was to find out whether the activity patterns of the major limb muscles were consistent with the two mechanisms proposed for storage and recovery of energy within a stride: a 'pendulum-like' mechanism during a walk, and a 'spring-like' mechanism during a run.

In the stance phase of the walking dog, we found that the supraspinatus, long head of the triceps brachii, biceps brachii, vastus lateralis, and gastrocnemius underwent only minor length changes during a relatively long portion of their activity. Thus, a major part of their activity during the walk seems consistent with a role in stabilization of the joints as the dog 'pole-vaulted' over its limbs (and thereby conserved energy).

In the stance phase of trotting and/or galloping dogs, we found that the supraspinatus, lateral head of the triceps, vastus lateralis, and gastrocnemius were active while being stretched prior to shortening (as would be required for elastic storage of energy), and that this type of activity increased with increasing speed.

We also found muscular activity in select limb flexors that was consistent with storage of kinetic energy at the end of the swing phase and recovery during the propulsive stroke. This activity pattern was apparent in the latissimus dorsi during a walk and trot, and in the biceps femoris during a trot and gallop.

We conclude that, during locomotion, a significant fraction of the electrical activity of a number of the dog's limb muscles occurs while they undergo little or no length change or are being stretched prior to shortening and that these types of activities occur in a manner that would enable the operation of pendulum-like and spring-like mechanisms for conserving energy within a stride. Therefore these forms of muscular activity, in addition to the more familiar activity associated with muscle shortening, should be considered to be important during locomotion.

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INTRODUCTION

One generally thinks of muscles as force generating elements that shorten to bring about the observed movements of the limbs, body and trunk during normal locomotion. Recent studies of the mechanics and energetics of terrestrial locomotion point to the importance of muscular activity while muscles remain the same length or are being stretched (Cavagna, Saibene & Margaria, 1963, 1964; Heglund, 1979; Heglund et al. 1979). In this study we set out to analyse the relative importance of these different types of muscular activities in a series of extensors and flexors of the limbs as dogs increased speed within a gait and changed gait.

The relative importance of the different types of muscular activity should change as animals change gait due to changes which occur in the mechanics of locomotion. A walking animal pole-vaults over its rigid limb in a manner analogous to an inverted pendulum. There is an alternate exchange between kinetic energy of its centre of mass in the forward direction and gravitational potential energy as the animal rotates over its rigid limb. As much as 60–70 % of the absolute changes in kinetic and gravitational energy of the centre of mass within each stride are conserved by this inverted pendulum mechanism (Cavagna & Kaneko, 1977; Cavagna, Heglund & Taylor, 1977; Heglund, 1979). In order for this mechanism to operate, some extensors must be active with minimal changes in length to keep the joints rigid as the animal rotates over its limbs.

Trotting, hopping, and galloping seem to involve a spring-like mechanism. The animal simultaneously breaks its fall and decelerates during one part of the stride, and then reaccelerates and lifts its centre of mass during another part. Energy appears to be stored by stretching active muscles and tendons as the animal decelerates and breaks its fall and then recovered as it reaccelerates upwards and forwards (Alexander & Vernon, 1975; Cavagna et al. 1977; Heglund, 1979). Some extensor muscles at each of the limb joints must be active when the animal lands to allow elastic energy to be stored in the muscles and tendons.

Another possibility for storage and recovery of elastic strain energy in muscles and tendons occurs as the limbs are alternately accelerated and decelerated relative to the centre of mass. The kinetic energy contained in the accelerated limb could be stored in muscles and tendons as the limb slows and reverses direction. This type of storage and recovery of energy could occur at all speeds in the muscles which reverse the limb direction.

Although these ideas about muscular activity have not been tested directly, they are consistent with published data from kinematic and electromyographic studies during quadrupedal locomotion. A number of limb extensor muscles have been shown to be active for joint stabilization during walking in rats (Cohen & Gans, 1975), cats (Goslow, Reinking & Stuart, 1973; English, 1978; Rasmussen, Chan & Goslow, 1978), and dogs (Tokuriki, 1973a; Wentink, 1976). Also some limb flexor and extensor muscles become active prior to limb reversal (cf. Engberg & Lundberg, 1969; Goslow et al. 1973). The present study set out to test these ideas about muscle activity directly by simultaneously measuring electrical activity and length of a series of extensor and

flexor muscles of the fore- and hindlimbs of dogs as a function of speed and gait. Use of a variable speed treadmill allowed for the analysis of a large number of successive and stable strides of select speeds and gaits.

MATERIALS AND METHODS
Animals

We selected dogs as experimental animals because they are extremely tractable, and because we had made measurements of mechanical work, mechanical power output and metabolic power input (Cavagna *et al.*, 1977; Heglund *et al.*, 1979; Taylor, 1978, 1980) on individuals that were available for these studies. Two mongrel dogs (1 female, 1 male, *Canis familiaris*, 20 kg) were used in these experiments. They were fed commercially available diets supplemented with vitamins and calcium. The dogs were housed in large indoor cages with adjoining outdoor runs. Both dogs ran on a treadmill regularly over a period of several years before the experiments. Our measurements were made while the animals ran at a constant speed on a treadmill for nine speeds (3 within a walk, 3 within a trot, and 3 within a gallop).

Muscles

We selected muscles for study that would test our ideas about holding the limb rigid during a walk, operating a limb-spring mechanism during a trot, and storing elastic energy during the end of the swing phase. Supraspinatus, triceps brachii (long and lateral heads), gluteus medius, vastus lateralis and gastrocnemius (medial and lateral heads) were chosen to study the possible role of joint extensors in the elastic storage of energy during locomotion. These particular muscles represent extensors of the shoulder, elbow, hip, knee and ankle respectively. Biceps brachii, brachialis and sartorius were selected to study the role of limb flexors during the swing phase. Latissimus dorsi and biceps femoris were chosen to study the possible role of elastic storage of energy in limb muscles that are capable of decelerating the limbs at the end of the swing phase.

Electromyography

A small patch of the dog's skin was shaved over the muscles to be studied. The area was cleaned with alcohol, lidocaine hydrochloride was injected under the skin, and a small incision was made. The electrodes were implanted and sutured in place. The local anaesthesia was adequate to prevent discomfort to the animal. A ground electrode coated with EKG electrode jelly was taped to a shaved area at the base of the tail. Placement of the electrodes was verified *before* and *after* each experiment by back stimulation and palpation. Recordings were made from a minimum of six separate electrode placements within each muscle of each dog. Four to thirty-eight strides were analysed from each placement.

The electrical activity of the muscles was recorded from electrodes made of 51 μm OD wire with a resistance of 700 Ω.m^{-1} (Evanohm's, Wilber B. Driver Co., Newark, NJ). The electrodes were constructed by placing a loop of wire through the barrel of a 23-gauge needle. The loop was cut and two millimetres of insulation were burned off the ends of the wire. The wire was bent backwards forming two hooks such that

the bare ends were approximately four millimetres apart. The signals obtained from the electrodes were first amplified by a set of EMG preamplifiers attached to the dog. The signal was then carried by co-axial cable to Grass EMG amplifiers (Model P511) and filtered for 60 Hz noise. The output of these amplifiers was connected to a 4-channel Tektronix storage oscilloscope (Series 5000). The EMG signals were recorded using an FM tape recorder (Bell & Howell CPR 4010). The tape recordings were played back on a multichannel strip chart recorder for analysis (Brush Gould, Model 260).

The electrical activity of the muscles was analysed only for duration of activity, i.e. on and off. The means and ranges for on and off were determined for four to thirty-eight sequential strides in each experiment.

Cinematography

Sixteen millimetre cine films were synchronized with the EMG recordings using an Eclair GV-16 cine camera. The cine films were taken at framing rates of between 50 and 200 frames/s. The limb angles and limb excursions were analysed by projecting the cine film onto a ground glass screen, and tracing the dog's outline frame by frame for a series of strides. A celluloid model of the major limb bones was constructed with movable joints. It was placed over the drawings to determine the limb angles. The angles were compared on ten separate drawings at each speed to determine their reproducibility. The values obtained using this method agreed well with independent measurements of shoulder angles made using high speed cineradiography where the bones could be visualized, eliminating the need for the celluloid model (pers. comm. F. A. Jenkins, Jr.). Relative muscle lengths were determined frame by frame during the stride by using a celluloid model on which the appropriate origin and insertion had been marked.
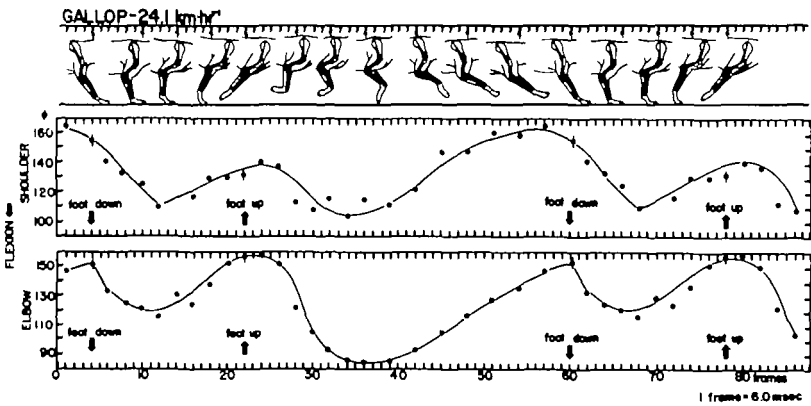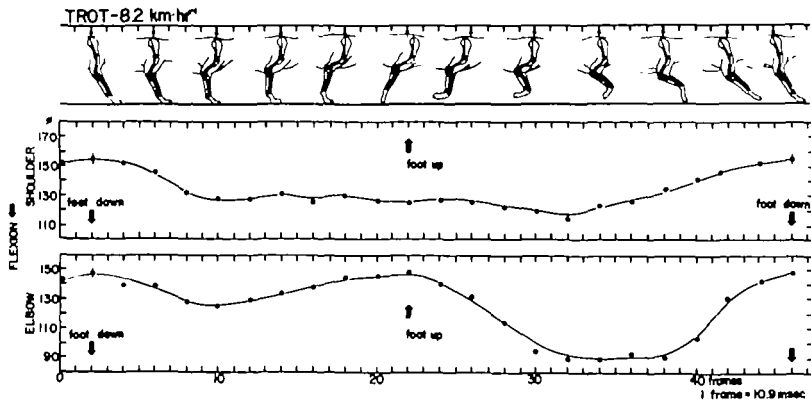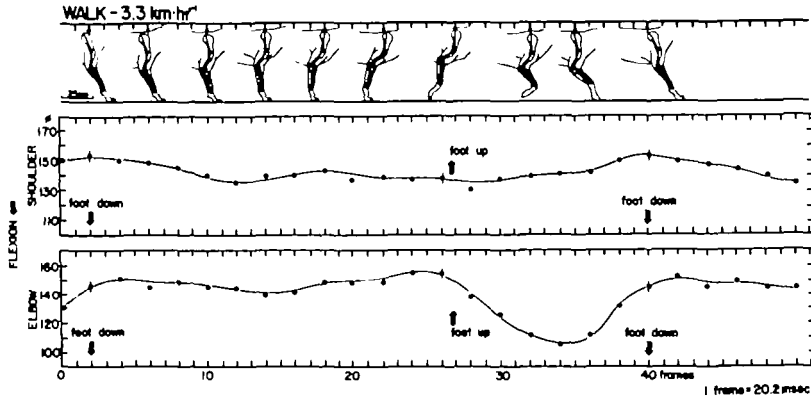
RESULTS

In the series of figures that follow, we present our measurements of electrical activity of muscles (EMGs) from the forelimb and hindlimb together with a measure of changes in muscle length. Measurements were made for three walking, three trotting, and three galloping speeds. Representative records are presented for one mid-speed within each gait. Means and ranges of the onset and termination of electrical activity are given. The angle of the joint around which a muscle operates is plotted for each of the muscles that acts only around a single joint. These angles allow one to determine whether the muscle-tendon unit was shortening, lengthening, or staying the same length during the time it was active. For those muscles that act around

Fig. 1. Forelimb joint angle changes during stepping. Top right: skeletal representation of the shoulder (scapulohumeral) and elbow (humeroulnar and humeroradial) joints measured in this study. Angles plotted for dogs walking ($3\cdot3$ km.h^{-1}), trotting ($8\cdot2$ km.h^{-1}) and galloping ($24\cdot1$ km.h^{-1}) on a treadmill. Note horizontal series of skeletal diagrams for visual cue of limb configuration on this and subsequent figures; small arrow notes exact film frame of drawing. Numbers on the ordinate indicate joint angle in degrees; flexion of both joints results in a decrease in angle. Note frame number from film on the abscissa and time reference (far right). Heavy arrows indicate the beginning of the stance phase (foot-down) and the beginning of the swing phase (foot-up). The small bar above and below the joint angle points at foot-down and foot-up represent the range of angles for ten successive strides.

Front limb angles

25 cm

WALK - 3.3 km·hr⁻¹

SHOULDER

FLEXION ⟸

170
150
130
110

foot up

foot down

foot down

ELBOW

160
140
120
100

foot down

foot up

foot down

0   10   20   30   40 frames

1 frame = 20.2 msec

TROT - 8.2 km·hr⁻¹

SHOULDER

FLEXION ⟸

170
150
130
110

foot up

foot down

foot down

ELBOW

150
130
110
90

foot down

foot up

0   10   20   30   40 frames

1 frame = 10.9 msec

GALLOP - 24.1 km·hr⁻¹

SHOULDER

FLEXION ⟸

160
140
120
100

foot down

foot up

foot down

foot up

ELBOW

150
130
110
90

foot down

foot up

foot down

foot up

0   10   20   30   40   50   60   70   80 frames

1 frame = 6.0 msec

two joints it was necessary to plot change in muscle length directly to obtain this information.

The joint angles for both the shoulder and the elbow are given in Fig. 1 and the EMGs of the front limb muscles that we measured are given together with the appropriate angle or length in Figs. 2–7. The joint angles for the hip, knee, and ankle are given in Fig. 8, and the EMGs of the hindlimb muscles that we measured are given together with the appropriate angle or length in Figs. 9–13. The data for each muscle are preceded by a description of its anatomical position and a statement of its function as inferred from this position (after Miller, Evans & Christensen, 1979). Such a statement provides a basis for comparison with our results and emphasizes the value of the present approach for determining muscle function.

Shoulder and elbow angles

These are given in Fig. 1 for dogs walking (3·3 km.h⁻¹), trotting (8·2 km.h⁻¹) and galloping (24·1 km.h⁻¹) on a treadmill. Shoulder flexion after foot-down and shoulder extension in the last half of the swing phase are characteristic of the walk and trot. Shoulder movements during galloping, however, contrast in both their temporal pattern and extent. In addition to the post-foot-down flexion and late swing phase extension movements of the slower gaits, extension during the second half of the stance and flexion in early swing also occur. Elbow flexion after foot lift-off and extension prior to foot down are characteristic of the swing phase at all gaits. In addition, a period of early stance phase elbow flexion occurs. This flexion is slight in the walk, more pronounced in the trot and distinct in the gallop.

M. supraspinatus

This is a single-joint muscle arising from the supraspinous fossa and cranial border of the scapular spine (Fig. 2). This muscle inserts by a strong tendon on the cranial border of the greater tubercle of the humerus (see drawing, top of Fig. 2). Its function, inferred from its anatomical position, is extension of the shoulder joint and forward advancement of the limb. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle stabilized and prevented collapse of the shoulder joint when the limb was bearing weight. At a walking speed of 3·2 km.h⁻¹ the muscle became active just after the foot touched the ground and remained active for 80% of the stance phase (or 54% of the total stride period). The shoulder flexed 15° during this period of electrical activity. Thus the muscle lengthened slightly while it was active. The pattern of activity was similar at different walking speeds.

Trot. The muscle stabilized, and prevented collapse of the shoulder joint when the limb was bearing weight. At a trotting speed of 8·3 km.h⁻¹ the muscle became active just after the foot touched the ground and remained active for 66% of the stance phase (or 33% of the stride period). During the activity the shoulder flexed by 20°. The pattern of activity was similar as trotting speed increased from 6·6 to 11 km.h⁻¹.

Gallop. The muscle provided some stabilization of the shoulder joint and assisted in its extension during the stance phase. The muscle became active just after foot-down and was stretched (allowing elastic storage of energy to take place), then it shortened and aided in shoulder extension at the end of the stance (providing pro
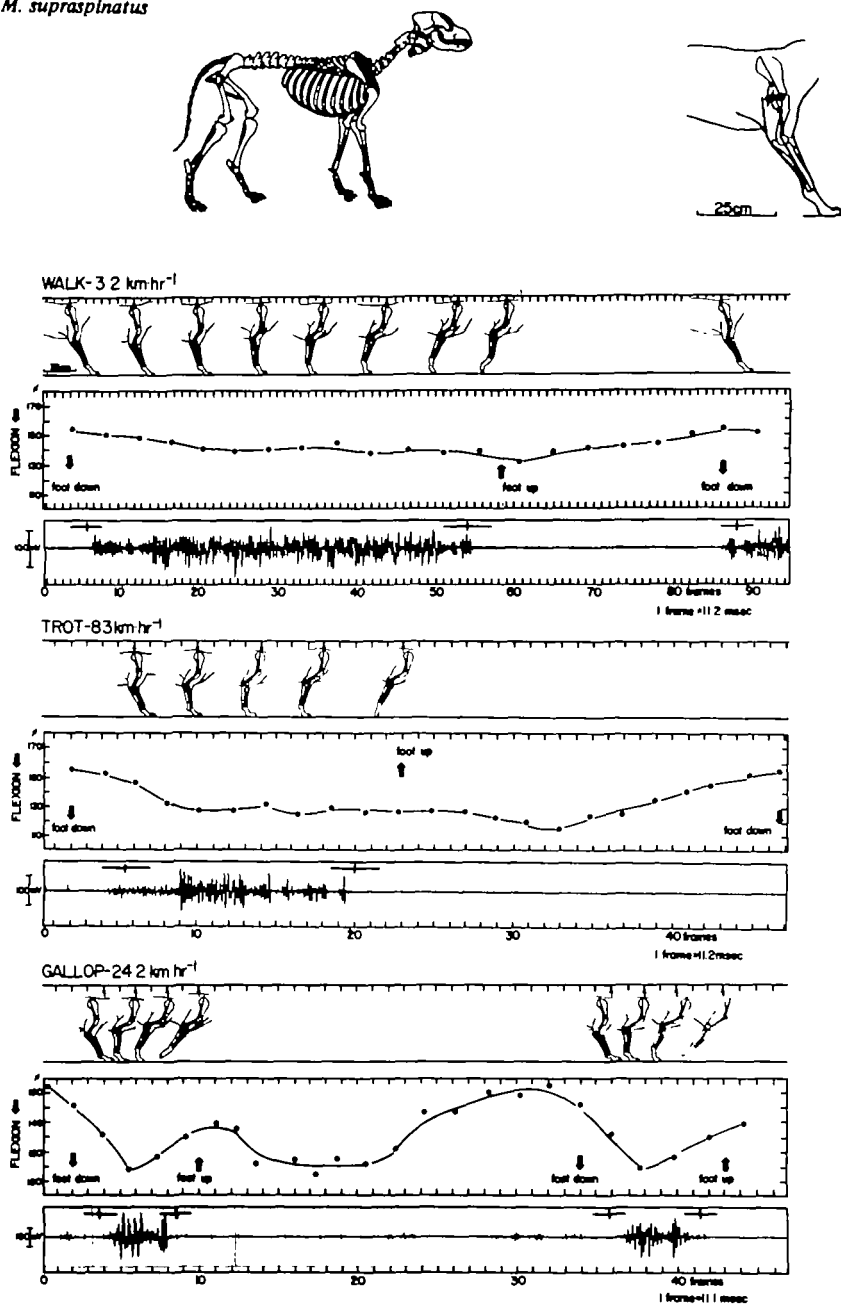
M. supraspinatus

Fig. 2. Typical electromyograms of the m. supraspinatus and shoulder angle during walking, trotting and galloping. Top left: muscle position indicated on the skeleton for this and subsequent figures. Top right: joint angle (s) noted around which the muscle acts for this and subsequent figures. Horizontal skeletal diagrams correspond to periods of muscle activity in the step cycle. Short vertical and horizontal bars on the EMG records represent means and ranges of onset and termination of muscle activity of records for 18–20 strides from two dogs. Note amplitude scale.

M. triceps brachii, caput laterale
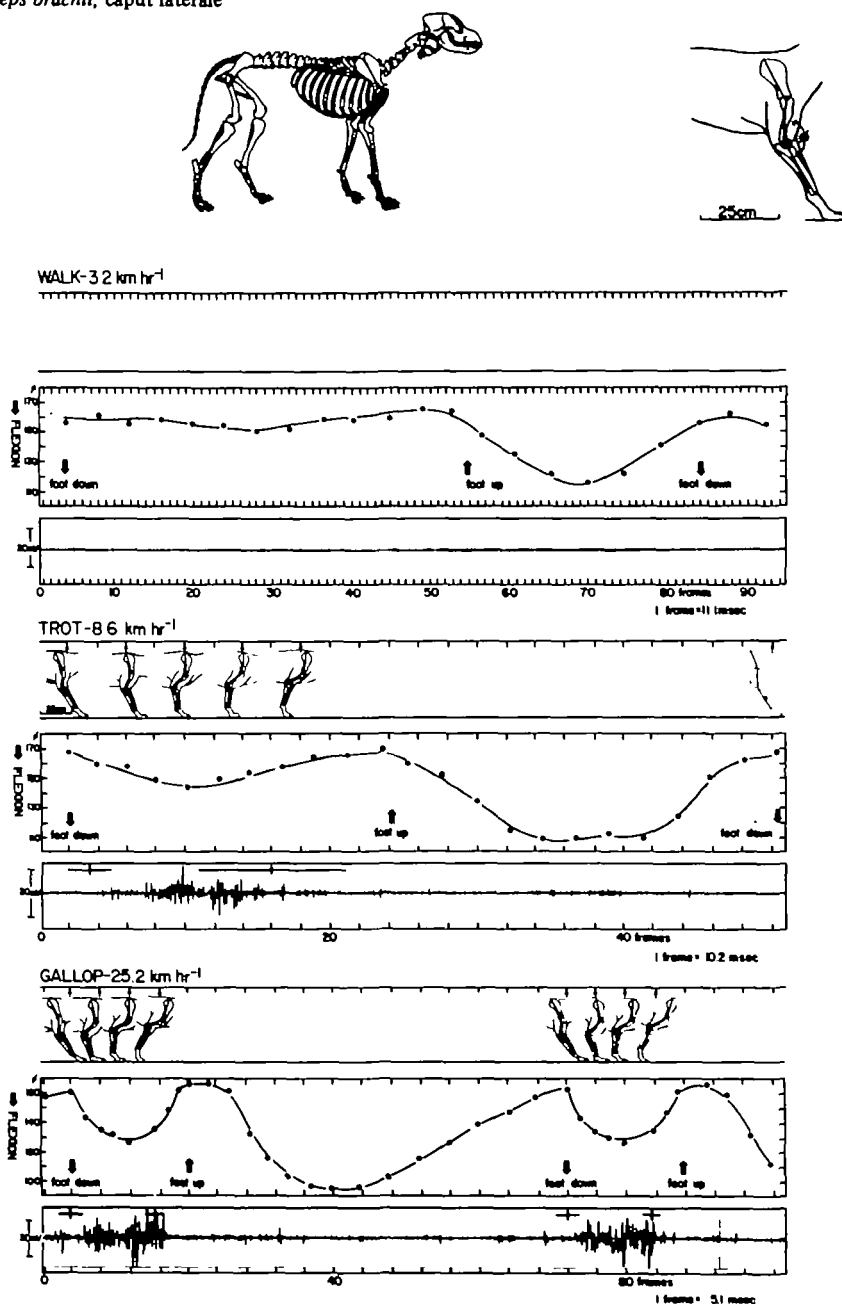
Fig. 3. Electromyograms of m. triceps brachii (caput laterale) and shoulder angle during walking, trotting and galloping. For notations see legend for Fig. 2. Short vertical and horizontal bars on the EMG records represent means and ranges for onset and termination of muscle activity for 22–32 strides from two dogs.

pulsion and allowing for recovery of stored elastic energy). At a galloping speed of 24·2 km.h⁻¹ the muscle was active for 65 % of the stance phase (or 18 % of the total stride period). During the period of activity the shoulder alternately flexed 22° and extended 22°. The pattern of activity was similar as the animal doubled its speed within a gallop.

M. triceps brachii (caput laterale)

This is a single-joint muscle which arises by an aponeurosis from most of the tricipital line on the lateral surface of the humerus (Fig. 3). The muscle inserts by a broad tendon on the olecranon process of the ulna. Its function, inferred from its anatomical position, is extension of the elbow. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle was not active.

Trot. The muscle was active while being stretched when the dog landed (preventing collapse of the elbow joint and allowing elastic storage to take place). Then it shortened and assisted in elbow extension in late stance phase (providing propulsion and allowing for recovery of stored elastic energy). At a trotting speed of 8·6 km.h⁻¹, the lateral head of the triceps became active just as the foot touched the ground. It remained active for 64 % of the stance phase (33 % of the stride period). During this activity, the elbow alternately flexed 20° and then extended 12°. The pattern of activity was similar as trotting speed increased from 6·1 to 11·0 km.h⁻¹.

Gallop. The muscle was active while being stretched when the dog landed (preventing collapse of the elbow joint and allowing elastic storage of energy to take place). In late stance the muscle shortened and assisted elbow extension (providing propulsion and allowing for recovery of stored elastic energy). At a galloping speed of 25 km.h⁻¹ the muscle became active just as the foot touched the ground and remained active for 70 % of the stance phase (20 % of the stride period). During activity, the elbow alternately flexed 35° and extended 15°. The pattern of activity was similar as the animal doubled its speed within a gallop.

M. triceps brachii (caput longum)

This is a two-joint muscle which arises from the distolateral two-thirds of the caudal border of the scapula (Fig. 4). This muscle inserts by a robust, round tendon on the caudal olecranon process of the ulna. Its function, inferred from its anatomical position, is extension of the elbow. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle stabilized and prevented collapse of the elbow joint when the limb was bearing weight. At a walking speed of 3·3 km.h⁻¹ the long head of the triceps became active at or just before foot down. The muscle remained active about 69 % of the stance phase (or 45 % of the stride period). The muscle shortened by about 5 % during the time it was active. This shortening was due to a flexion of the shoulder joint which more than compensated for the flexion of the elbow (Fig. 1). The pattern of activity was the same at different walking speeds.

Trot. The muscle stabilized and prevented collapse of the elbow joint after the foot made contact with the ground, initiated elbow extension, and provided a propulsive force during the last part of the stance phase. At a trotting speed of 8·2 km.h⁻¹, the muscle became active just before the foot touched the ground. The muscle remained
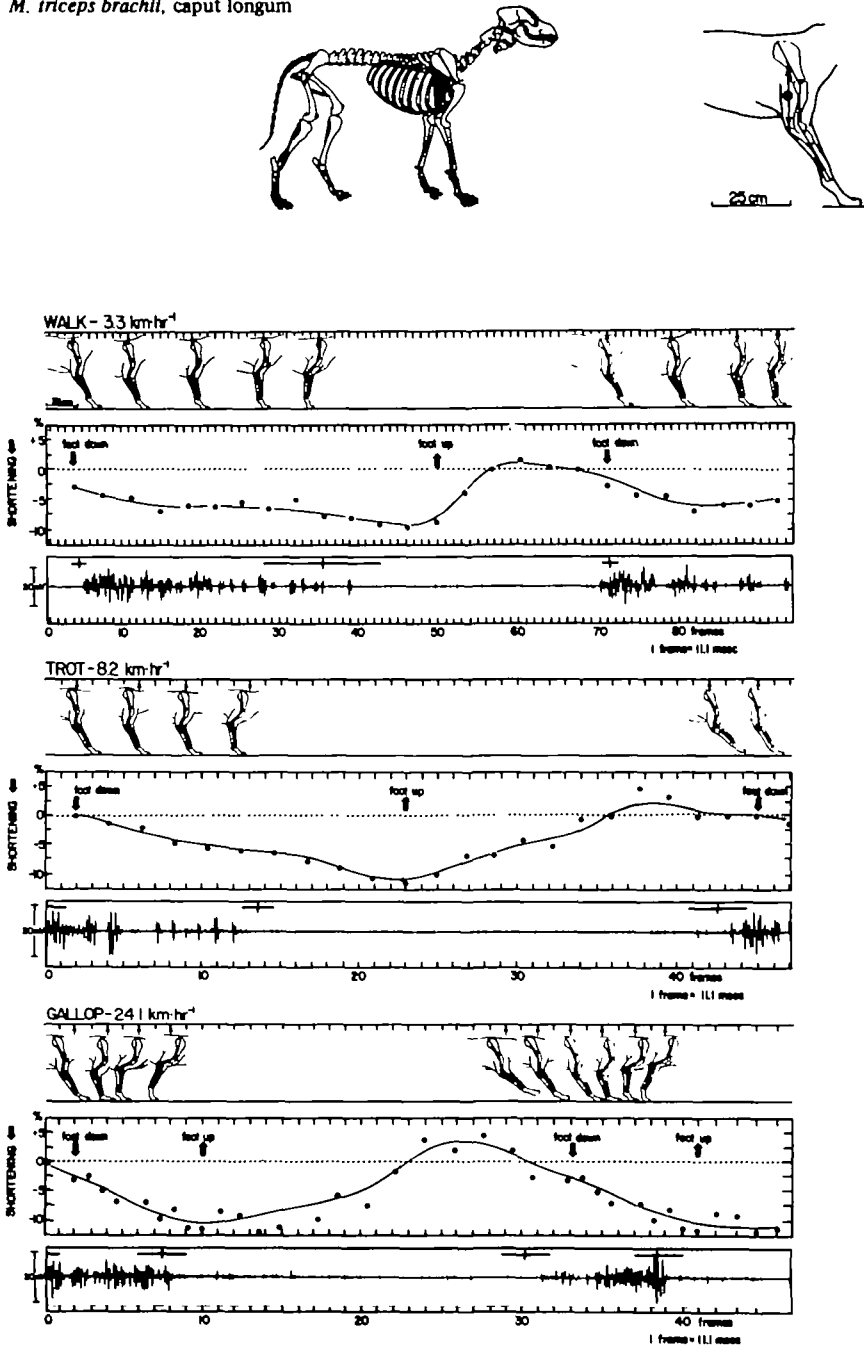
M. triceps brachii, caput longum

Fig. 4. Electromyograms and changes in length of m. triceps brachii (caput longum) during walking, trotting and galloping. Muscle length is given as a percentage of standing length. For notations see legend for Fig. 2. Vertical and horizontal bars on EMG records represent means and ranges of onset and termination of muscle activity for 15–17 strides from two dogs.

active for about 47 % of the stance phase or about 28 % of the stride. The muscle shortened by about 7 % while it was active. This shortening was due first to a flexion of the shoulder joint (which more than compensated for the flexion of the elbow) and then an extension of the elbow (Fig. 1). The pattern of activity was similar as trotting speed increased from 6·6 to 11·0 km.h^{-1} except for the period of activity before the foot touched the ground which increased from 0 to about 50 msec.

Gallop. The muscle assisted elbow extension just before the foot contacted the ground, stabilized and prevented collapse of the elbow joint after the foot first made contact with the ground, and initiated elbow extension providing a propulsive force while the foot was in contact with the ground. At a galloping speed of 24·1 km.h^{-1}, the long head of the triceps became active just before the foot touched the ground and remained active for 70 % of the stance phase or 32 % of the stride. During the activity when the foot was on the ground, the muscle shortened by about 8 %. After the foot touched the ground the elbow began to flex, but this was more than compensated for by flexion of the shoulder. The muscle continued its activity while the elbow began to extend, providing some propulsion (Fig. 1). The pattern of activity was similar as the animal doubled its speed within a gallop.

M. latissimus dorsi

This originates as an aponeurosis from the lumbodorsal fascia of the caudal seven or eight thoracic vertebrae and all of the lumbar vertebrae (Fig. 5). In addition, muscular slips of origin arise from the proximolateral surface of the last two or three ribs. The insertion of this muscle is complex. In addition to a tendinous insertion at the teres tubercle on the medial side of the humerus, fascial slips of the muscle join the medial triceps and deep pectoralis. Its function, inferred from its anatomical position, is to draw the limb backwards and to pull the trunk forward over the supported limb. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle pulled the trunk forward over the supported limb and decelerated the forward movement of the free limb. The activity of this muscle was biphasic. The major period of activity occurred during the stance phase. At a walking speed of 3·2 km.h^{-1}, the muscle became active and began to pull the trunk forward over the supported limb after about 44 % of the stance phase was completed. It then remained active, shortened by 10 %, and provided propulsion for about 46 % of the stance phase. There was a second short burst of activity just before and after the foot touched the ground as the muscle decelerated the forward movement of the limb. This activity lasted for about 7 % of the stride period. The muscle lengthened by about 10 % as it decelerated forward movement of the free limb. The pattern was similar at all walking speeds.

Trot. The muscle pulled the trunk over the supported limb, decelerated the forward movement of the free limb (allowing elastic storage of kinetic energy) and reaccelerated the limb backwards (allowing recovery of the stored energy). The activity of the muscle was still biphasic during a trot. At a trotting speed of 8·2 km.h^{-1}, the muscle became active and began to pull the trunk forward over the supported limb for about 49 % of the stance phase (33 % of the total stride period). During the second period of activity, the muscle first decelerated the forward movement of the limb, and then
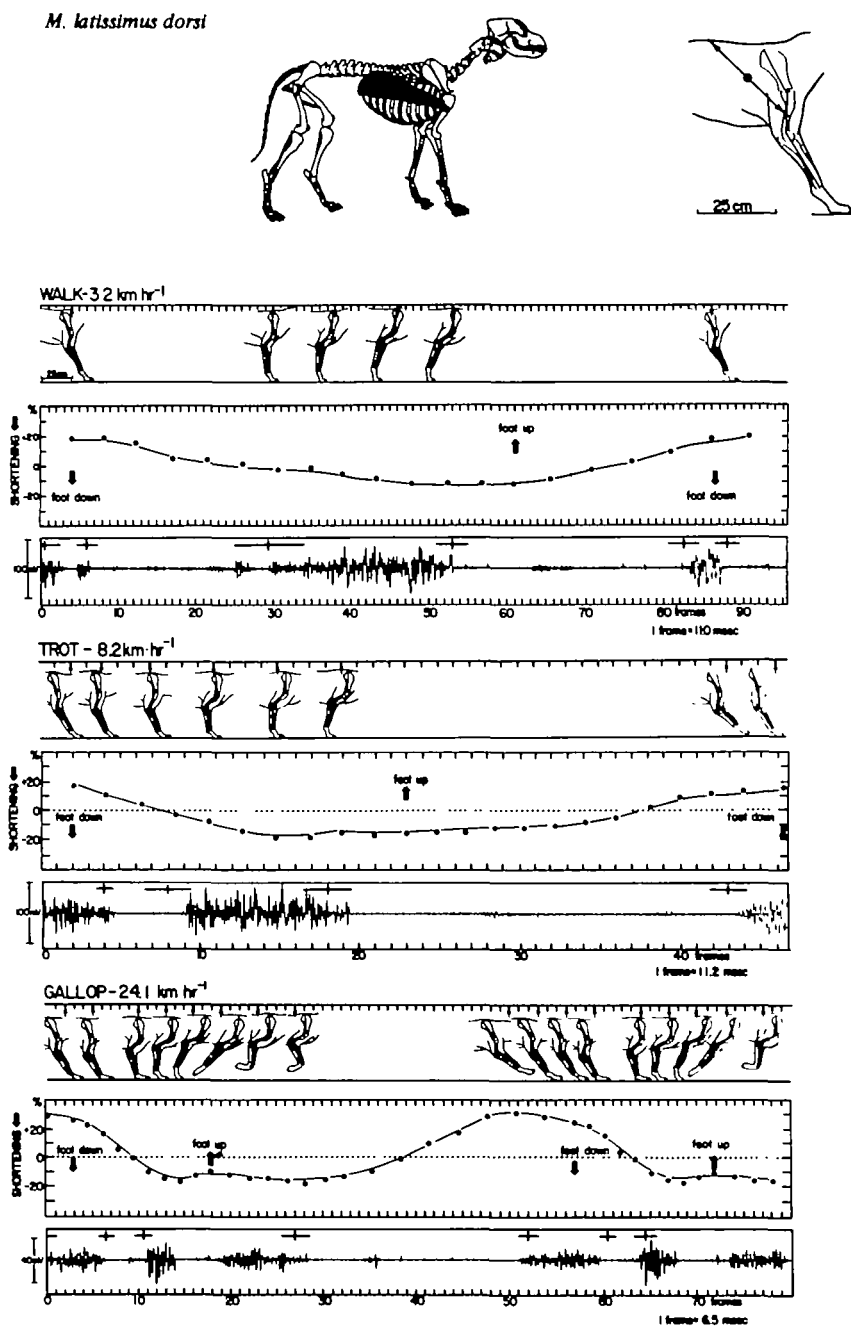
Fig. 5. Electromyograms and changes in length of m. latissimus dorsi during walking, trotting and galloping. For notations see legends for Figs. 2 and 4. Short vertical and horizontal bars on the EMG records represent means and ranges for onset and termination of muscle activity for 9–15 strides of one dog.

initiated the acceleration of the limb in the opposite direction. This burst of activity lasted about 11% of the total stride period. During a complete stride the muscle alternately shortened and lengthened by about 10%. The pattern of activity was similar at different trotting speeds.

Gallop. The muscle pulled the trunk forward over the supported limb, accelerated the free limb backwards before and just after the foot touched the ground, and, during an additional third phase of activity added in the gallop, it supported the free limb during the initial part of the swing phase. At a galloping speed of 24·1 km.h⁻¹, the muscle became active and began to pull the trunk forward over the supported limb after about 50% of the stance phase was completed. It then remained active for the remainder of the stance during the propulsive stroke. It continued its activity after the foot left the ground, supporting the free limb during the initial part of the swing phase. Sometimes there was a pause between the propulsive and support phases (Fig. 5) and at other times the activity was continuous. Both phases accounted for about 32% of the total stride period. The muscle shortened by about 40% as it provided propulsion and its length was then unchanged while it supported the free limb. The pattern of activity was similar at different galloping speeds.

M. biceps brachii

This is a two-joint muscle which originates by a strong tendon from the tuber scapula (coracoid process) (Fig. 6). Distally the tendon of insertion divides: the more robust of the two inserts on the ulna tuberosity and the other on the radial tuberosity. Its function, inferred from anatomical positions, is flexion of the elbow joint. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle stabilized and prevented collapse of the shoulder joint when the limb was bearing weight, and assisted in elbow flexion during the swing phase. At a walking speed of 3·2 km.h⁻¹ the muscle became active after about 37% of the stance phase was completed. It remained active for the remainder of the stance phase and 43% of the following swing phase. The activity lasted 57% of the stride period. The muscle remained about the same length while it was active during the stance phase and then shortened by about 15% during the swing phase as the elbow flexed (Fig. 1). The pattern of activity was similar at different walking speeds.

Trot. The muscle stabilized and prevented collapse of the shoulder joint when the limb was bearing weight. At a trotting speed of 8·2 km.h⁻¹, the muscle became active after about 46% of the stance phase was completed and continued its activity for the remainder of the time the foot was on the ground and 7% of the following swing phase (30% of the total stride). The muscle lengthened by about 5% during the stance phase due to extension of the elbow (Fig. 1). The pattern of activity was essentially the same at different trotting speeds.

Gallop. The muscle stabilized and prevented collapse of the shoulder joint when the limb was bearing weight, and provided for elbow flexion during the swing phase. At a galloping speed of 24·1 km.h⁻¹, the muscle became active after about 56% of the stance phase was completed and continued its activity for the remainder of the time the foot was on the ground and 16% of the following swing phase (23% of the total stride). The active muscle lengthened by about 10% during the late stance phase and
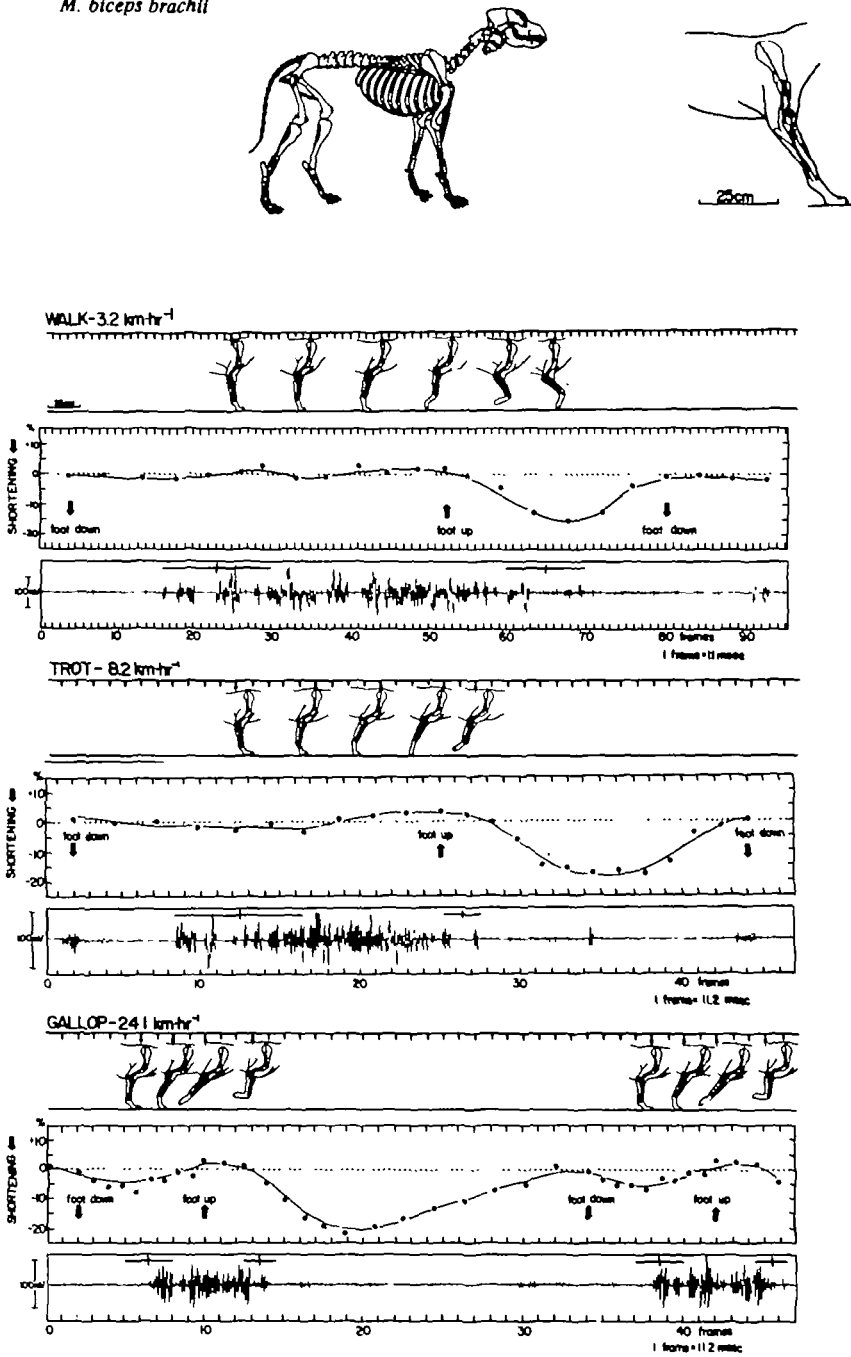
M. biceps brachii

Fig. 6. Electromyograms and changes in length of m. biceps brachii during walking, trotting and galloping. For notations see legends for Figs. 2 and 4. The vertical and horizontal bars on the EMG records represent the means and ranges for onset and termination of activity for 29–37 strides from one dog.
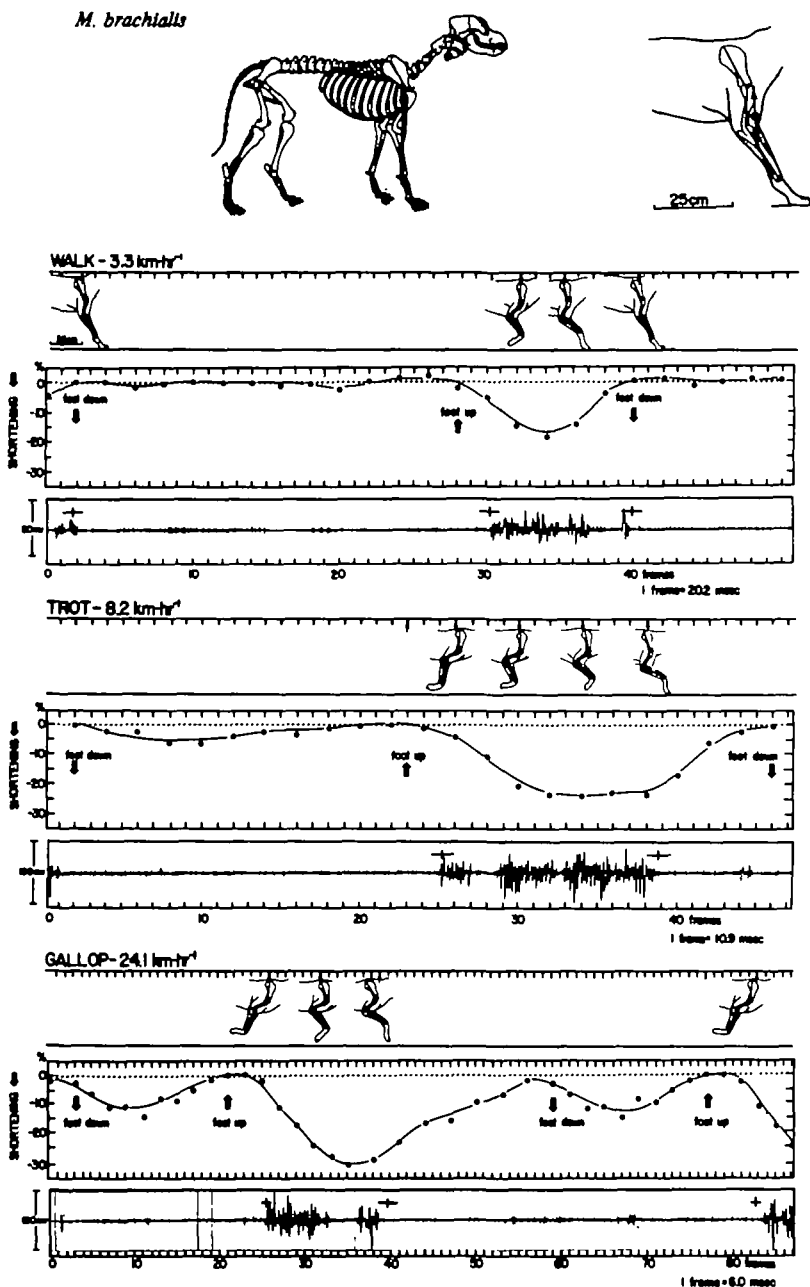
Fig. 7. Electromyograms for m. brachialis and elbow angle during walking, trotting and galloping. For notations see legends for Fig. 2. Vertical and horizontal bars on the EMG records represent means and ranges for onset and termination of muscle activity for 14 strides from two dogs.

then alternately shortened and lengthened by about 20 % during the swing phase due
to extension and flexion of the elbow (Fig. 1). The pattern of activity was similar at
different galloping speeds.

M. brachialis

This is a single-joint muscle which originates from the proximal part of the caudal
surface of the humerus (Fig. 7). Distally the muscle has a dual insertion, some fleshy
fibres end on the tendon of the m. biceps brachii coursing to the radial tuberosity, and
a distinct tendon inserts on the ulnar tuberosity. Its function, inferred from its
anatomical position, is flexion at the elbow. Our data suggest the following action
based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle flexed the elbow joint during swing phase to decelerate an
extension of the elbow prior to foot-down. At a walking speed of 3·3 km.h⁻¹ the
muscle became active about 30 msec after the foot left the ground and remained active
for 87 % of the swing phase. The muscle was active for about 28 % of the stride period.
The active muscle alternately lengthened and shortened as the elbow flexed and
extended by about 50° during the swing phase. The pattern of activity was similar at
different walking speeds.

Trot. The muscle flexed the elbow and maintained the joint in a flexed position
prior to extension (little if any involvement in the control of extension during late
swing phase). At a trotting speed of 8·2 km.h⁻¹ the muscle became active about
21 msec after the foot left the ground and remained active for 61 % of the swing phase.
The muscle was active for about 32 % of the stride period. The elbow flexed by about
60° during the first half of its activity and maintained this flexed position during the
remainder of the time it was active. The pattern of activity was similar at different
trotting speeds.

Gallop. The muscle flexed the elbow (little if any involvement in control of exten-
sion). At a galloping speed of 24·1 km.h⁻¹ the muscle became active 27 msec after
the foot left the ground and remained active for 42 % of the swing phase. The muscle
was active for 29 % of the total stride. The elbow flexed by about 66° and extended by
about 10° during the time the muscle was active. The pattern of activity was similar
at different galloping speeds.

Joint angles of the hip, knee, and ankle

These are given in Fig. 8 for dogs walking (3·3 km.h⁻¹), trotting (8·2 km.h⁻¹) and
galloping (24·1 km.h⁻¹) on a treadmill. At all gaits the hip (iliofemoral) begins slight
extension in late swing prior to foot-down. At foot-down, the hip generally stabilizes
before it begins gradual extension during the remaining stance phase. When the foot
is lifted off the ground, the hip begins flexion which continues until the late swing
phase extension begins. Flexion-extension movements of the knee and ankle are
essentially in phase for the three gaits. At foot-down, both joints flex in early stance
before they begin extension coincident with propulsion. This early flexion (the 'yield')
is slight in walking, moderate in the trot, and distinct in the gallop. Foot lift-off is
characterized by knee and ankle flexion which continues to about mid-swing. Both
joints extend in the second half of the swing in anticipation of foot-down.

M. gluteus medius

This is a single-joint muscle of extensive origin from the lateral aspect of the ilium (wing; gluteal surface) (Fig. 9). The muscle inserts by a strong tendon on the free end of the greater trochanter. Its function inferred from its anatomical position is extension of the hip joint. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle extended the hip. At a walk of 3·4 km.h^{-1} the muscle became active just before the foot touched the ground and remained active for 62 % of the stance phase (48 % of the stride period). The muscle shortened during the entire time it was active extending the hip by 30°. The pattern of activity was the same at different walking speeds.

Trot. The muscle extended the hip. At a trotting speed of 8·5 km.h^{-1} the muscle became active before the foot touched the ground and remained active for the first part of the stance phase. It was active for about 27 % of the stride period. The muscle shortened during the entire time it was active, extending the hip by about 15°. The pattern of activity was the same at different trotting speeds.

Gallop. The muscle extended the hip. At a galloping speed of 24·7 km.h^{-1} the muscle became active before the foot touched the ground and remained active for the first part of the stance phase. It was active for 25 % of the stride period. The muscle shortened during the entire time it was active, extending the hip by about 17°. The pattern of activity was the same at different trotting speeds.

M. vastus lateralis

This is a single-joint muscle arising on the craniolateral surface of the proximal fifth of the femur (Fig. 10). Distally this muscle's tendon of insertion fuses to that of the m. rectus femoris, m. vastus medialis and the m. tensor fasciae latae; the common tendon incorporates the patella before continuing to insert on the tibial tuberosity. Its function, inferred from anatomical position, is extension of the knee. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle stabilized the knee during most of the stance phase, then shortened, providing forward propulsion. At a walking speed of 3·1 km.h^{-1} the muscle became active just prior to foot-down and remained active for 81 % of the stance phase (58 % of the stride period). The muscle length was unchanged during most of its activity, stabilizing the knee, and then at the end of the stance phase it shortened and extended the knee by about 10°. The pattern was similar at all walking speeds.

Trot. The active muscle was first stretched after the foot touched the ground (allowing storage of elastic energy) and then shortened and extended the knee (allowing recovery of the stored elastic energy). At a trotting speed of 8·1 km.h^{-1} the muscle became active just before the foot touched the ground and remained active for 70 % of the stance phase (32 % of the stride period). The muscle stretched, then shortened as the knee alternately flexed and extended by 20°. The pattern of activity was the same at different trotting speeds.

Gallop. The active muscle was first stretched after the foot touched the ground and

Hind limb angles

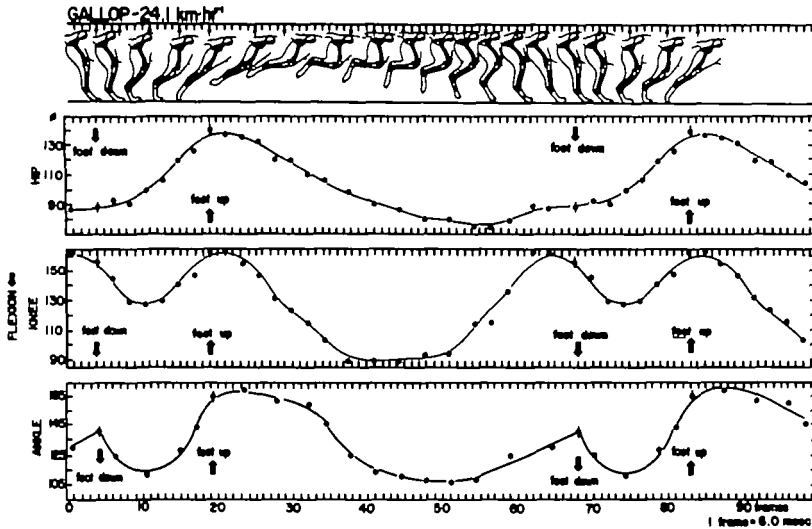WALK - 3.3 km·hr⁻¹

TROT - 8.2 km·hr⁻¹
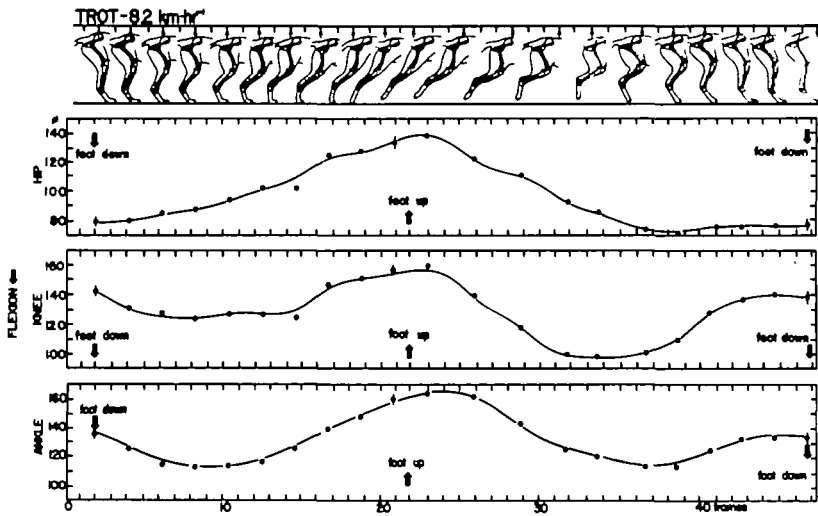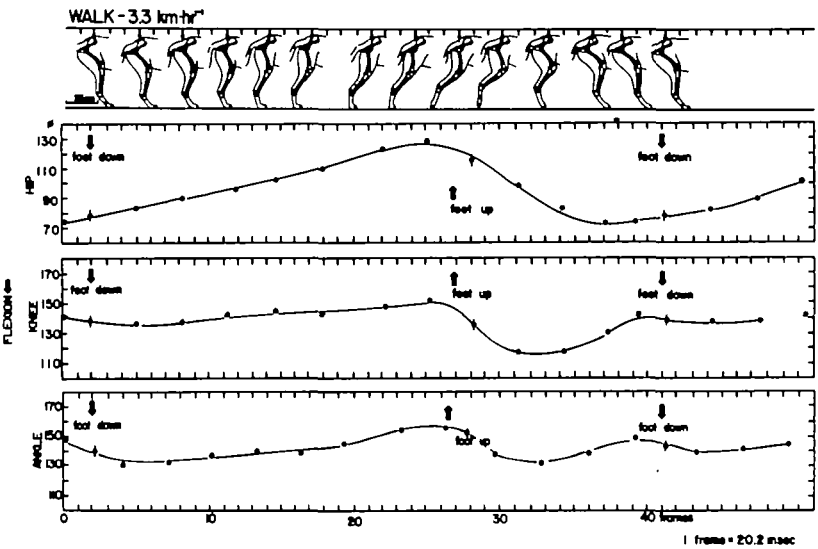
Fig. 8. Hindlimb joint angle changes during stepping. Hip, knee and ankle angles are plotted for dogs walking, trotting and galloping on a treadmill. For notations see legend of Fig. 1.

remained active for 94 % of the stance phase (25 % of the stride period). The muscle alternately lengthened and shortened during activity as the knee flexed and extended by 35°. The pattern of activity was similar at all galloping speeds.

M. gastrocnemius (medial head)

This is a two-joint muscle that arises from the medial supracondylar tuberosity of the femur. This muscle fuses with the lateral gastrocnemius through much of its length. Distally the tendon inserts on the tuber calcanei of the calcaneus. Its function, inferred from its anatomical position, is extension of the tarsal joint and flexion of the knee. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle extended and then stabilized the ankle during the stance phase. At a walking speed of 3·2 km.h^{-1}, the muscle became active at foot-down and remained active 81 % of the stance phase (58.% of the stride). Simultaneous knee and ankle flexion resulted in about a 9 % active length change in early stance. Muscle length remained about the same during subsequent knee and ankle extension in the late stance. The pattern of activity was similar at all walking speeds.

Trot. The muscle supported the ankle during early stance and extended the ankle in late stance. At a trotting speed of 7·8 km.h^{-1}, muscle activity commenced after foot-down and remained for 73 % of the stance phase (33 % of the stride). During the stance as the knee and ankle alternately flexed and extended the muscle actively shortened 15 % of its total length. The pattern was similar at other trotting speeds.

Gallop. The muscle supported the ankle during early stance phase ankle flexion (allows elastic storage) and extended the ankle, allowing recovery of elastic storage energy, during late stance. At a gallop of 24 km.h^{-1}, though muscle activity did not begin until after foot-down, the muscle was active during part of the very rapid flexion of the knee and ankle during the yield. The resulting activity of medial gastrocnemius
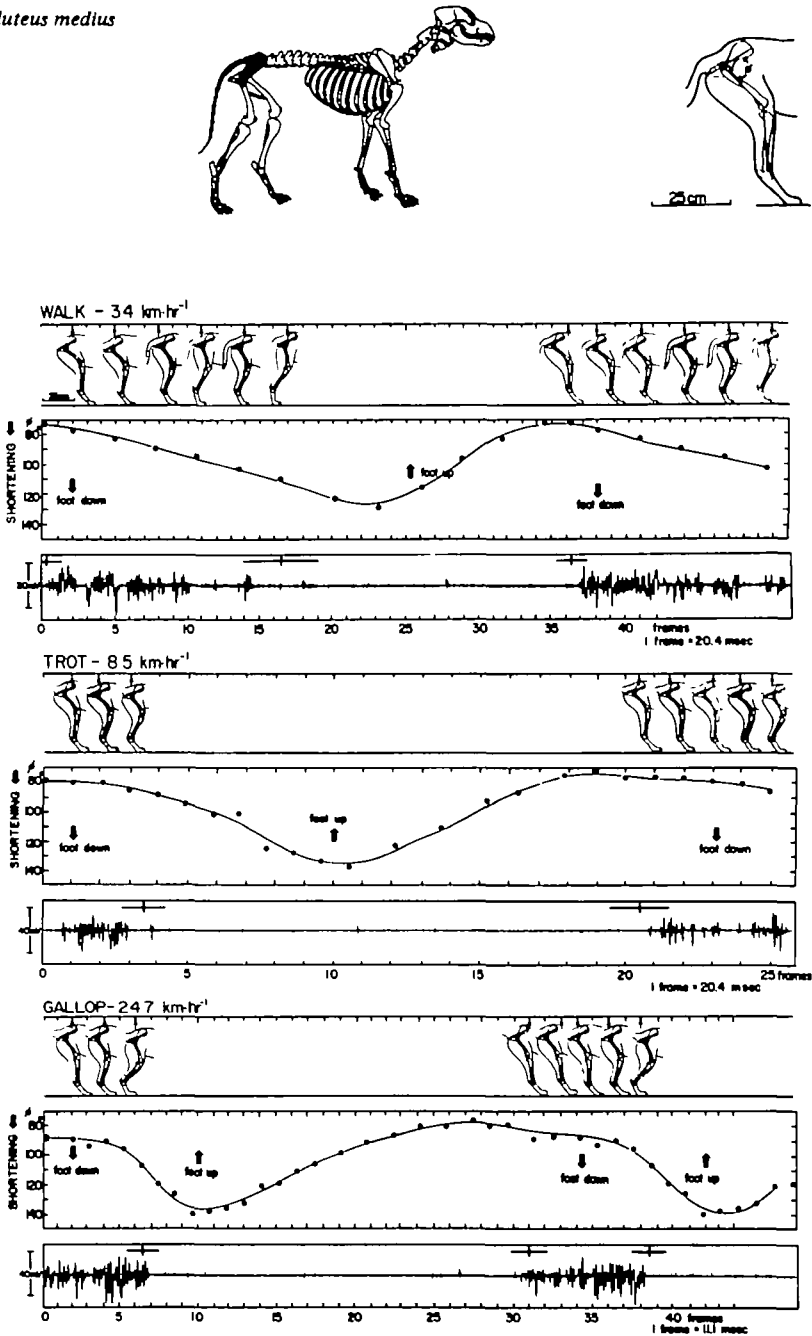
Fig. 9. Electromyograms for m. gluteus medius and hip angle during walking, trotting and galloping. For notations see legend for Fig. 2. The vertical and horizontal bars represent the means and ranges for onset and termination of activity for 15–22 strides on one dog.
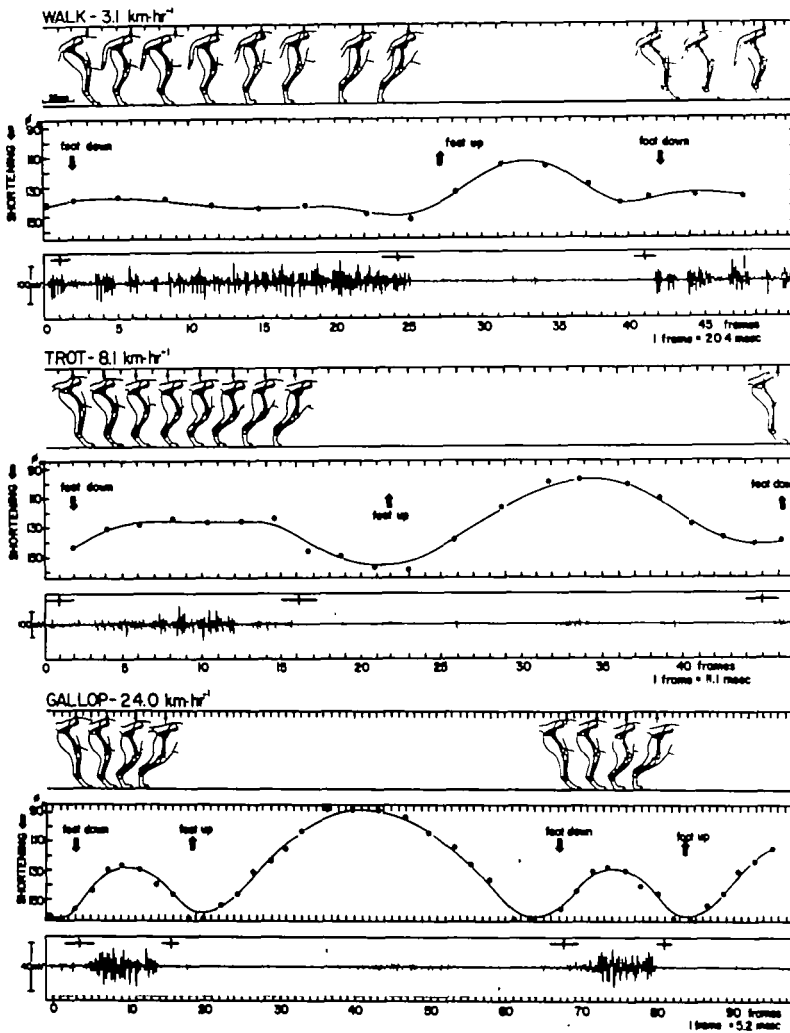
M. vastus lateralis

Fig. 10. Electromyograms for m. vastus lateralis and knee angle during walking, trotting and galloping. For notations see legend for Fig. 2. The vertical and horizontal bars represent the means and ranges for onset and termination of activity for 24–35 strides from two dogs.
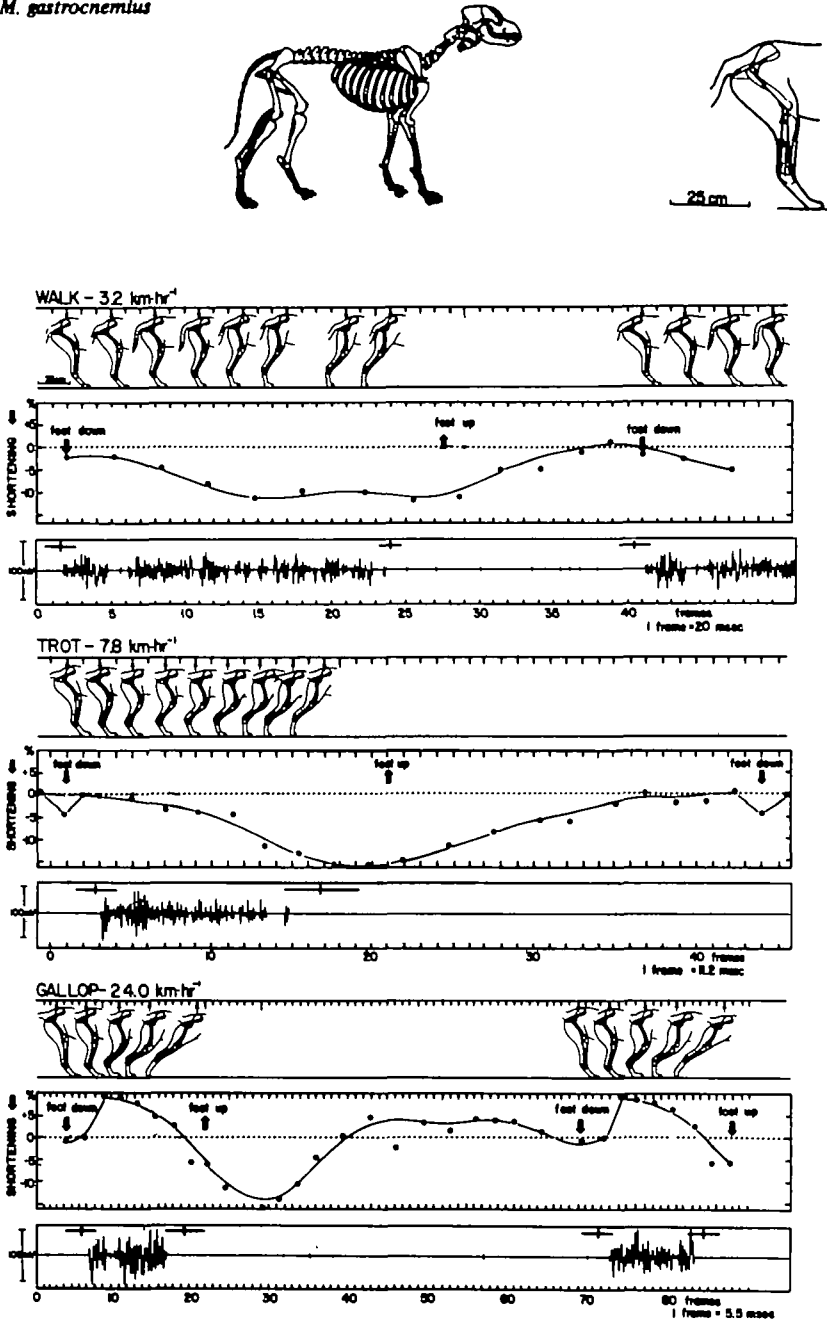
M. gastrocnemius

Fig. 11. Electromyograms and length changes for m. gastrocnemius (medial head) during walking, trotting and galloping. For notations see legends for Figs. 2 and 4. Vertical and horizontal bars on EMG records represent means and ranges for onset and termination of activity for 17–36 strides from two dogs.
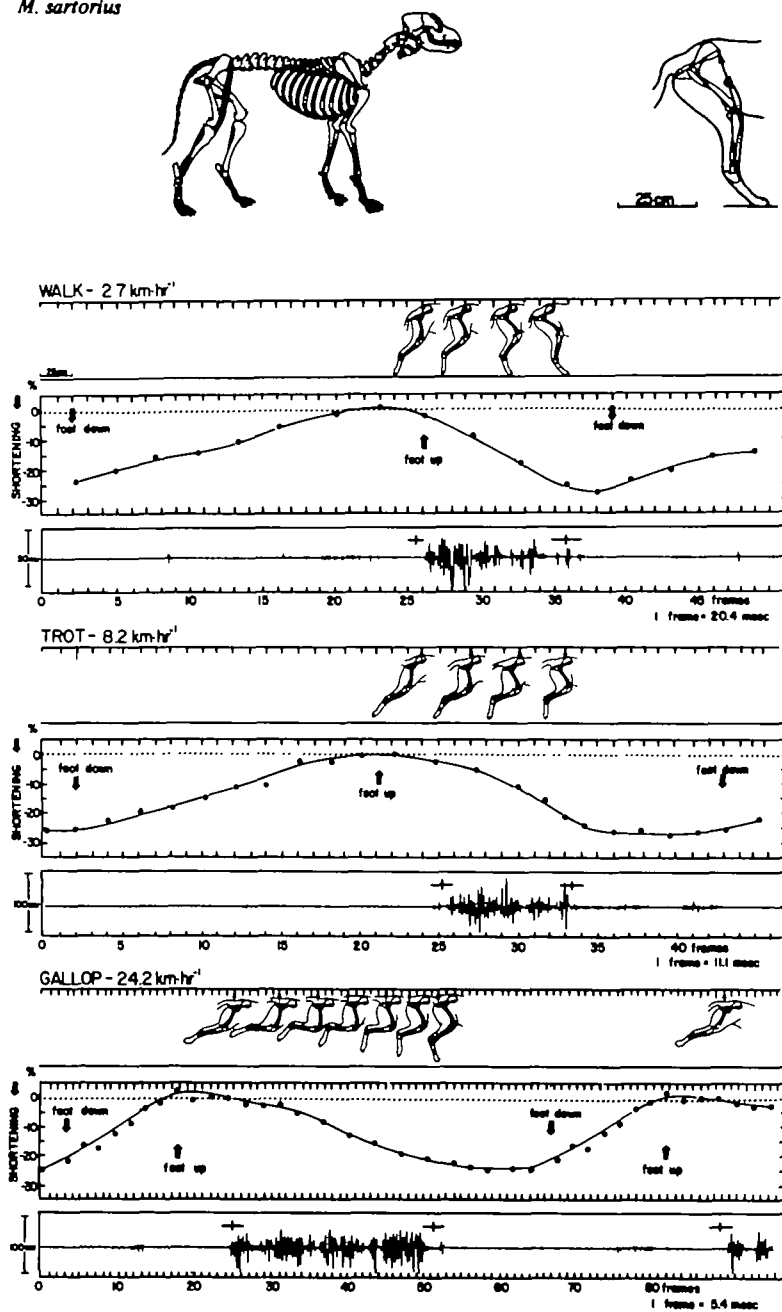
M. sartorius

Fig. 12. Electromyograms and changes in length for m. sartorius during walking, trotting and galloping. For notations see legends for Figs. 2 and 4. Vertical and horizontal bars represent means and ranges for onset and termination of activity for 14 strides from two dogs.

while the muscle is stretched resulted in some elastic storage. The muscle was active 88% of the stance phase (25% of the stride). During the yield, the muscle was actively stretched 9% of its length which was followed by active shortening of 10% corresponding to rapid extension of the knee and ankle. The pattern was similar at other galloping speeds.

M. sartorius (cranial belly)

This is a two-joint muscle arising from the cranial ventral spine of the iliac crest as well as from the lumbodorsal fascia (Fig. 12). The muscle belly passes medially along the thigh to a heavy fascia just proximal to the patella. The fascia ties tightly to the tendons of the m. rectus femoris and m. vastus medialis. Its function, inferred from its anatomical position, is flexion of the hip, extension and adduction of the thigh. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle flexed the hip. At a walking speed of 2·7 km.h^{-1} the muscle became active before the foot left the ground and remained active for 73% of the swing phase. The muscle was active for 27% of the stride period. The hip flexed by about 46° while the muscle was active: thus the muscle shortened by about 28% during its activity. The pattern of activity was the same at different walking speeds.

Trot. The muscle flexed the hip. At a trotting speed of 8·2 km.h^{-1} the muscle became active after the foot left the ground, and remained active for 38% of the swing phase. The muscle was active for 28% of the stride period. The hip flexed by about 57° while the muscle was active. The muscle shortened by about 22% during its activity. The pattern of activity was the same at different trotting speeds.

Gallop. The muscle flexed the hip. At a galloping speed of 24·2 km.h^{-1} the muscle became active after the foot left the ground and remained active for 55% of the swing phase. The muscle was active for 42% of the stride. The hip flexed by about 50° while the muscle was active. The pattern of activity was similar at different galloping speeds.

M. biceps femoris (cranial head)

This is a two-joint muscle (largest of the two heads) arising fleshy from the ventro-caudal end of the sacrotuberous ligament and the ischial tuberosity (Fig. 13). Distally the tendon of insertion appears as an aponeurosis, part of which inserts on the patella and part of which traverses to the tibial tuberosity. Two muscle lengths were analysed; a patellar aspect and tibial aspect. Its function, inferred from its anatomical position, is extension of the hip and knee when the limb is bearing weight. The tibial part of the muscles raises the leg when the limb is not bearing weight and therefore can flex the knee under these circumstances. Our data suggest the following action based on electrical activity and changes in length of the muscle during a stride.

Walk. The muscle extended the hip after the foot touched the ground. At a walking speed of 3·3 km.h^{-1} the muscle became active just before the foot touched the ground and remained active for 69% of the stance phase (56% of the stride period). The patellar portion of the muscle shortened by about 20% while the muscle was active due primarily to hip extension. Simultaneous knee flexion resulted in about a 10% active shortening of the tibial portion. The pattern of activity was similar at all walking speeds.

Trot. The muscle decelerated the forward movement of the limb before the foot
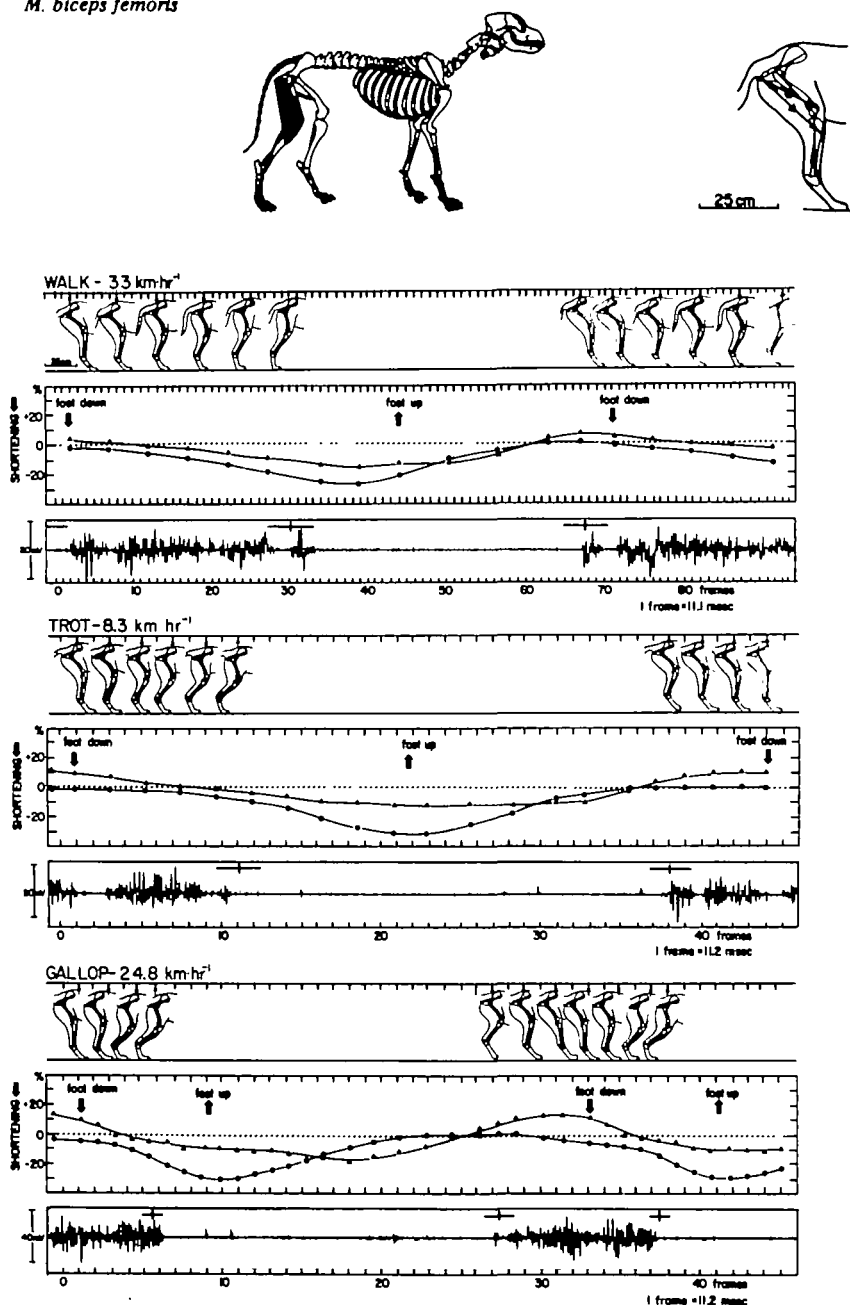
M. biceps femoris

Fig. 13. Electromyograms and changes in length for m. biceps femoris (cranial head) during walking, trotting and galloping. Two muscle lengths were analysed because of the muscle's broad insertion; a patellar aspect (solid circles) and a tibial aspect (solid triangles). For notations see legends for Figs. 2 and 4. Vertical and horizontal bars represent the means and ranges for onset and termination of activity for 13-15 strides from two dogs.

touched the ground, and extended the hip after the foot touched the ground. At a trotting speed of 8·3 km.h^{-1}, the muscle became active prior to foot-down (25 % of the swing phase) and remained active for about 46 % of the stance phase (34 % of the stride period). During the activity period prior to foot-down, the muscle decelerated the forward movement of the limb by slowing the rate of extension of the knee. Knee extension at this time resulted in stretch of the tibial portion of the active muscle (by about 10 % of its length) allowing for elastic storage of kinetic energy. Both portions of the muscle actively shortened by about 10 % after foot-down, providing forward propulsion and allowing recovery of the stored elastic energy. The stance phase shortening occurred when there was a simultaneous extension of the hip and flexion of the knee. However, flexion of the knee could occur passively due to the effects of gravity on the weighted limb. The pattern of activity was similar at all trotting speeds.

Gallop. The muscle decelerated the forward movement of the limb and reaccelerated it in the opposite direction before the foot touched the ground and extended the hip after the foot touched the ground. At a galloping speed of 24·8 km.h^{-1}, the muscle became active well prior to foot-down (27 % of swing phase) and remained active for 51 % of the stance phase (33 % of total stride period). The deceleration of the limb was due mainly to slowing the rate of knee extension, and the reacceleration of the limb in the opposite direction was due to both flexion of the knee and extension of the hip. During the deceleration phase, the tibial aspect was being actively stretched by about 10 %. After foot-down, the entire muscle shortened by about 15 %, due first to extension of the hip and flexion of the knee in early stance; then both portions continued shortening due to an extension of the hip which was more than sufficient to compensate a simultaneous extension of the knee in late stance. The pattern was similar at all galloping speeds.

DISCUSSION

In this analysis we set out to determine the relative importance of the three types of muscular activity (shortening, isometric and lengthening) as animals increase speed within a gait and as they change gait. In contrast to previous studies, we obtained a large number of synchronous joint angle and muscle activity measurements at a variety of speeds. These data were extremely reproducible because we used a treadmill where speeds could be replicated easily. Wetzel *et al.* (1975) compared limb joint angles and stride profiles of cats moving on a treadmill with cats moving overground. The analysis revealed the extension period of the swing phase to be significantly shorter for the treadmill cats than for the overground ones. The authors concluded the differences were due at least in part to the intimidating influence of the treadmill. We found that stride frequency, swing phase and support phase for our dogs were the same when they ran at the same speed along the ground and on the treadmill. This is probably the result of using dogs that were well trained for treadmill running.

Muscular activity for joint stabilization during a walk

We found that during a walk the electrical activity and length changes of a number of limb extensors are consistent with the interpretation that joint stabilization was a major function of these muscles during the period when the limb was bearing weight

This type of activity is necessary for the animal to 'pole-vault' over its limbs and thereby store and recover gravitational potential energy. Both the supraspinatus of the shoulder and the long head of the triceps and biceps brachii of the elbow underwent only minor length change ($\cong 5\%$) during their stance phase activity. In the hindlimb, the vastus lateralis and medial gastrocnemius were also active for large parts of the stance with little length change. Thus we conclude that one important role of these joint extensors during the walk is to provide joint stabilization. Not all extensors need contribute to such stabilization as is evidenced by a lack of activity of lateral triceps in the walk. These data are essentially in agreement with published findings for the walking dog (Tokuriki, 1973a; Wentink, 1976), cat (Engberg & Lundberg, 1969; English, 1978; Rasmussen *et al.*, 1978), Virginia opossum (Jenkins & Weijs, 1979) and rat (Cohen & Gans, 1975).

Muscular activity of limb muscles for elastic storage during a trot and a gallop

We found that some of the limb extensors are active while being stretched prior to shortening during a trot and gallop as would be required for elastic storage of energy when the animal lands. For review of this concept as related to locomotion in general and limb mechanics specifically, see Cavagna *et al.* (1964, 1977) and Goslow *et al.* (1973). This type of activity increased dramatically with increasing speed (both in duration and in amplitude of the EMG signal). In the forelimb we found this pattern of EMG activity as the muscles were stretched for the supraspinatus and for the lateral head of the triceps. The long head of the triceps, which acts across two joints, actively shortened during all of its activity. Some hindlimb muscles that we sampled also were alternately stretched and then shortened while they were active. The vastus lateralis was stretched and then shortened while active both during trotting and galloping and this activity pattern was consistent over a range of speeds. Activity of the gastrocnemius while being stretched and then shortening was consistently observed at fast trot and galloping speeds, but this pattern was inconsistent at slower trotting speeds. It seems possible that this inconsistency was due to compartmentalization of activity within the muscle at the slower trotting speeds. Compartmentalization has been observed in architecturally complex muscles such as the mammalian masseter (Herring, Grimm & Grimm, 1979).

Similar patterns of activity (i.e. limb extensors active while being stretched and then shortening) have been observed for the dog by Tokuriki (1973b, 1974) and for the cat by Engberg & Lundberg (1969), English (1978) and Rasmussen *et al.* (1978). It therefore seems likely that this 'bounce' spring function of extensors is probably general for quadrupedal mammals.

We also found a pattern of muscular activity in the limb flexors that would allow storage of kinetic energy at the end of the swing phase and recovery during the propulsive stroke. This was apparent in the latissimus dorsi during a walk and trot (but less clear in a gallop) and in the biceps femoris during a trot and a gallop. This type of activity was not observed in the biceps brachii, brachialis or satorius. Our data are consistent with those of Tokuriki (1973a, b; 1974) for a dog and with those of English (1978) and Rasmussen *et al.* (1978) for the cat.

CONCLUSION

We conclude that our electrical activity and length changes of the muscle measurements are consistent with the 'pole-vault' and 'spring mechanisms' for energy conservation proposed from studies of the mechanics and energetics of locomotion (Cavagna *et al.* 1963, 1964; Alexander & Vernon, 1975; Cavagna *et al.* 1977; Taylor, 1980).

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