

Locomotor function of the pectoral girdle 'muscular sling' in trotting dogs

David R. Carrier*, Stephen M. Deban and Timna Fischbein
Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

*Author for correspondence (e-mail: carrier@biology.utah.edu)

Accepted 22 March 2006

Summary

In therian mammals, gravitational and locomotor forces are transferred between the forelimb and trunk primarily, or entirely, through the muscles that connect the limb and trunk. Our understanding of this force transmission is based on analyses of shoulder anatomy and on a handful of descriptive electromyographic studies. To improve our understanding, we manipulated the locomotor forces of trotting dogs and monitored the resulting change in recruitment of five extrinsic muscles of the forelimb: *m. serratus ventralis thoracis*, *m. serratus ventralis cervicis*, *m. pectoralis superficialis transversus*, the anterior portion of the *m. pectoralis profundus*, and *m. rhomboideus thoracis*. Locomotor forces were modified as the dogs trotted at constant speed on a motorized treadmill by (1) adding mass to the trunk, (2) inclining the treadmill so that the dogs ran up and down hill, (3) adding mass to the wrists and (4) applying horizontally directed force to the trunk through a leash. These experiments indicate that the thoracic portion of the serratus ventralis muscle is the main antigravity muscle of the shoulder during trotting in dogs. Its activity increased when we added mass to the trunk and also when we ran the subjects downhill. In contrast, the cervical portion of the serratus ventralis did not show a consistent increase in

activity in response to added mass. Instead, its activity increased when we ran the subjects up hill and added mass to their wrists, suggesting that it functions to stabilize the fulcrum of the forelimb in the cranial-caudal direction during active retraction of the forelimb. The thoracic portion of the rhomboideus muscle also appears to provide this cranial-caudal stabilization during active retraction of the forelimb. The force manipulations indicate that the transverse pectoralis muscle acts to both protract and retract the forelimb, depending on the position of the limb. In contrast, the anterior portion of the pectoralis profundus muscle acts as a retractor of the forelimb during the end of swing phase and the beginning of support phase. We found that adding mass to the trunk did not increase the activity of forelimb retractor muscles, suggesting that the ground reaction force vector passes through, or very near, the fulcrum of the shoulder during a trotting step. Whether or not the functions of these extrinsic appendicular muscles in dogs characterize therian mammals or represent specializations for high-speed, economical running remains to be determined.

Key words: serratus ventralis, pectoralis, rhomboideus, EMG, recruitment, quadruped, running, shoulder.

Introduction

The shoulder girdle of therian mammals (marsupials and placentals) is unique among tetrapods both in its structure and in its great mobility. In contrast to the shoulder of their therapsid ancestors, the shoulder of therians lacks the procoracoid, has a dramatically reduced coracoid, has a glenoid that faces ventrally rather than laterally and posteriorly, and has a mobile clavicle linking the sternum and scapula (Romer, 1956; Jenkins and Weijjs, 1979). The reduction of the coracoids and the mobility of the clavicle effectively eliminate the firm skeletal attachment between the shoulder and sternum that was present in basal therapsids. This allows the scapula to both rotate and translate in the plane in which the forelimb swings, such that the scapula functions as the proximal skeletal element and center of rotation of the forelimb (Gray, 1968; Fischer et

al., 2002). Associated with the enhanced mobility of the shoulder is an increased reliance on extrinsic appendicular muscles for support of body weight and transmission of locomotor forces and moments between the trunk and forelimb. Although joint fulcra are usually defined by the articulations of skeletal elements, in the therian shoulder the position of the fulcrum is a function of the level of activity of the various extrinsic shoulder muscles and the moment on the limb.

Two sets of muscles may be involved in support of body weight at the shoulder in therian mammals. During a walking or running step, support of body mass can be partially accomplished by extrinsic appendicular muscles of the shoulder that have orientations appropriate for protraction or retraction of the limb. At times when the ground reaction force

and the inertia and mass of the limb exert a net protracting moment at the shoulder, muscles that have an orientation appropriate for forelimb retraction must be active to resist collapse of the limb at the shoulder. Similarly, muscles that have an ability to protract the limb must help support body weight when there is a net retracting moment on the shoulder. Additionally, because there is no rigid skeletal connection between the sternum and scapula, muscles with a vertical orientation, which link the forelimb and trunk, must be active to support body weight and define the fulcrum of the shoulder. It is this latter set of shoulder muscles, with anatomy appropriate for resisting gravity that is often referred to as the 'muscular sling' of the pectoral girdle (Kardong, 1998).

Five extrinsic muscles of the shoulder have attachment sites and vertical orientations that would allow support of body weight: cervical and thoracic portions of the serratus ventralis, transverse and deep pectoralis and rhomboideus (Fig. 1). Some authors have suggested that the serratus ventralis muscle is primarily or entirely responsible for supporting body mass at the forelimbs (Davis, 1949; Gray, 1968). Its spatial configuration, spanning the distance between the cervical transverse processes and sternal ribs to the dorsomedial aspect of the scapula, makes it ideally suited for this purpose. Nevertheless, recordings of muscle activity in walking opossums (Jenkins and Weijs, 1979) and running cats (English, 1978) show that the pectoralis and rhomboid muscles are active during the first half of limb support in a manner consistent with a role in vertical support. Thus, the current literature does not adequately answer the question of which muscles support body weight at the shoulder of therian mammals.

The question of which muscles support body weight at the shoulder has relevance to the evolution of the therian pectoral girdle, the manner in which moments and forces are transferred between the forelimb and trunk, the function of the axial muscles in providing postural stabilization of the trunk during locomotion, and the integration of locomotion and lung ventilation in mammals. These are all issues that cannot be adequately addressed without a clearer understanding of the function of the extrinsic muscles of the forelimb.

In this investigation, we studied the locomotor function of the five muscles that are often suggested to resist the force of gravity at the shoulder of therian mammals. We monitored changes in the recruitment of these muscles in response to controlled manipulations of locomotor forces and moments. The rationale of the method is that changes in forelimb mechanical requirements must be met by correlated changes in the recruitment of the muscles that transmit forces and

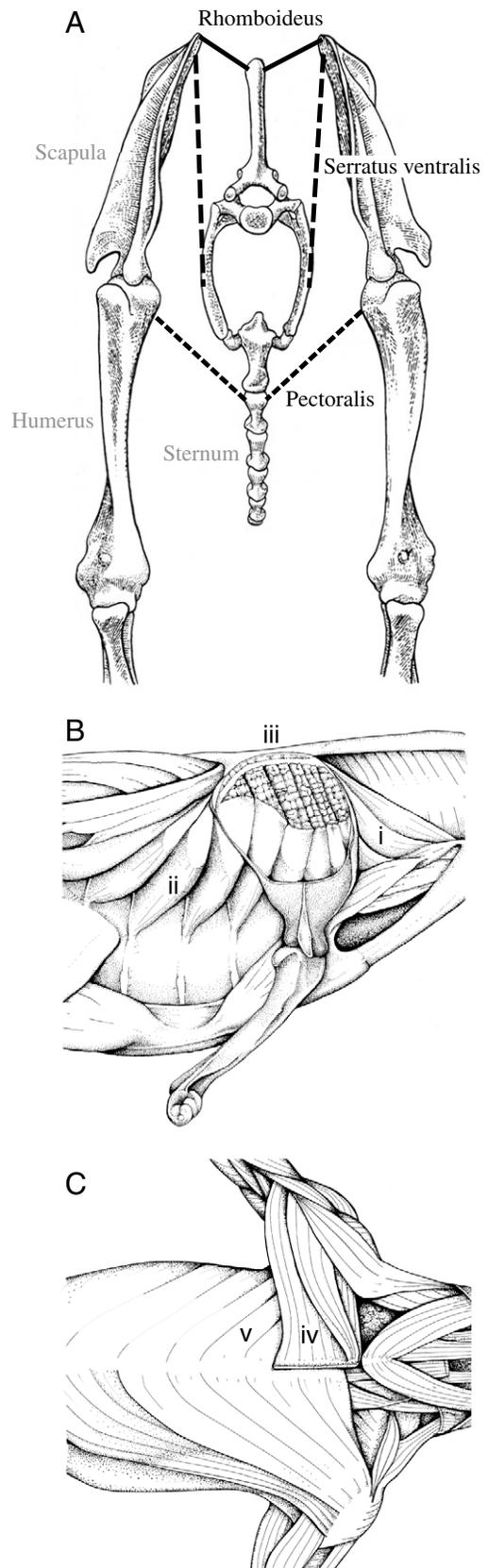


Fig. 1. Illustration of the muscular sling of the pectoral girdle of therian mammals. (A) Schematic representation of the three primary components of the muscular sling. Muscles are represented by solid and broken lines, and labeled in black type; bones are labeled in grey type. Modified from (Davis, 1949). (B) Lateral view of the m. serratus ventralis muscle showing position of the electrodes in, the m. serratus ventralis cervicalis (i), m. serratus ventralis thoracis (ii) and the m. rhomboideus thoracis (iii). (C) Ventral view of the m. pectoralis muscle showing the position of the electrodes in, the m. pectoralis superficialis transverses (iv) and m. pectoralis profundus (v).

moments between the forelimb and trunk. Hence, we interpret changes in muscle recruitment associated with the manipulations of locomotor forces and moments to reflect a functional role for the muscle.

Materials and methods

Activity of five extrinsic appendicular muscles of the forelimb was monitored in six mixed-breed dogs (*Canis lupus familiaris* Linnaeus 1753) while they trotted at moderate speed (approximately 2 ms^{-1}) on a motorized treadmill. The muscles studied were the m. pectoralis superficialis transversus, the anterior aspect of the m. pectoralis profundus, the m. serratus ventralis thoracis inserting on ribs 5 and 6, the m. serratus ventralis cervicis inserting on the transverse processes of C6, and the m. rhomboideus thoracis located directly medial to the dorsal margin of the scapula (Fig. 1B,C). The anatomy of these muscles is described elsewhere (Evans, 1993). Mean body mass of the six dogs was $24 \pm 4.2 \text{ kg}$ ($\pm \text{ s.d.}$). Each dog was obtained from a local animal shelter and trained to run on a treadmill. Recording of muscle activity began on the fourth day after surgery and continued for 5–6 days. The electrodes were removed 10 or 11 days after implantation. After a period of recovery, each dog was adopted as a pet. All procedures conformed to the guidelines of the University of Utah Institutional Animal Care and Use Committee.

Instrumentation

For surgery, subjects were initially anesthetized with an intravenous injection of Pentethal to effect. They were then intubated with an endotracheal tube and maintained on a ventilator with oxygen to 1.3 MAC and 1–2% isoflurane for the duration of the surgery. Incisions were made through the skin above the site of electrode placement and sew-through electrodes were secured to the muscles of interest. Two sew-through electrodes (Basmajian and Stecko, 1962) were implanted at each site to provide redundancy in case of electrode failure. Electrodes were constructed from 0.3 mm, multistranded Teflon insulated stainless steel wire (Cooner Wire, Inc., Chatsworth, CA, USA; part no. AS636). Lead wires from the electrodes were passed subcutaneously to a dorsal exit point just caudal to the point where the scapula spine intersects the dorsal margin of the scapula. Electromyographic signals were passed through a separate shielded, lightweight cable for each electrode (Cooner Wire, Inc. Part no. NMUF2/30-404b SJ), filtered above 1000 Hz and below 100 Hz, and amplified approximately 2000 times with Grass P511 AC amplifiers. These signals were sampled at 4000 Hz and stored in digital form on an Apple Macintosh computer.

To associate muscle activity with phases of limb support, locomotor events were recorded on video at 60 Hz with a high-speed camera (Peak Performance Technologies, Inc., Centennial, CO, USA). An analog signal of the locomotor cycle was obtained by monitoring the vertical acceleration of the trunk with an accelerometer (Microtron, 7290A-10,

Endevco Corp., San Juan Capistrano, CA, USA) mounted on the dorsal surface of the dog's back in the mid-lumbar region. The video recordings were synchronized with the electromyogram (EMG) and accelerometer recordings using a circuit that illuminated a LED in the video field while simultaneously introducing a square wave into one channel of the EMG recording system.

Locomotor force manipulations

To improve our understanding of the locomotor function of the five muscles we monitored changes in EMG patterns in response to manipulations of the locomotor forces. (1) To increase the vertical forces on the forelimbs due to gravity, the dogs ran with a backpack containing mass of 0% (control), 8% and 12% of body mass. These masses were carried in four different positions on a dog's back, representing four different trials: added mass carried over the pectoral girdle (anterior-trunk mass); over the middle of the trunk (mid-trunk mass); over the pelvic girdle (posterior-trunk mass); and the added mass split in two equal portions and carried over the pectoral and pelvic girdles (anterior/posterior mass). (2) To increase the fore-aft forces required to accelerate and decelerate the mass of the body during a running step, we inclined the treadmill so that the dogs ran both up and down hill at slopes of 0° (control), 10° and 14° from the horizontal. When the dogs ran uphill, the incline increased the positive (propulsive) work the dog had to do in the fore/aft direction. When the dogs ran downhill, the incline increased the negative (braking) work the dog had to do in the fore/aft direction. In addition to changing the positive and negative propulsive-braking work, the incline running altered the relative distribution of gravitational loads on the forelimbs and hindlimbs. (3) We also manipulated the fore/aft and lateral forces by applying horizontally oriented forward-, backward-, rightward- and leftward-directed forces on the dogs as they ran on a level treadmill. These forces were applied to the dogs with a handheld leash that was attached to the dogs *via* a muzzle over the dog's snout for the forward-directed pulls, with a sled racing harness for the rearward-directed pulls, and a with a loop around the neck and another loop around the dog's trunk at the abdomen for the rightward- and leftward-directed forces. The muzzle was a greyhound racing muscle that allowed the dogs to pant as they ran. The leash was attached to the front of the muzzle so that the pulling force was applied through the occipital strap of the muzzle to the back of the dog's head. These horizontal forces were increased and decreased by manual manipulation. The applied force was monitored with a force transducer that was in-series with the leash. The output of the force transducer was recorded digitally and was displayed on an oscilloscope so that the experimenter could adjust the level of force. (4) To increase the forces required to protract and retract the forelimbs during a running step, we added mass of 0% (control), 1% and 2% of body mass to the dog's wrists. Running speed was held constant through the control and experimental trials of a given force manipulation.

Analysis of electromyographic data

To examine the relationship between muscle recruitment and locomotor events, we generated average EMGs for each muscle from 20 samples (strides) (Banzett et al., 1992a; Banzett et al., 1992b). These 'stride averages' were generated from rectified EMGs using a sampling window, identified with the acceleration signal. The sampling window began and ended with the initiation of ipsilateral limb support. The video recordings were used to identify the point in the accelerometer signal that represented touchdown of the ipsilateral forelimb. The sampling window varied slightly in duration and consequently differed in the number of recorded data points. To enable averaging across multiple samples (strides) of different durations, each EMG sample was normalized using a custom LabVIEW program to generate a new sample consisting of 120 bins in which all the point values from the original EMG sample were partitioned. For example, the first of the 120 bins contained the sum of the point values from the original sample that occurred in the first 120th of the stride. Likewise, the second bin contained the sum of the point values from the second 120th of the stride, and so on. Stride averages were then generated by averaging the value for each of the 120 bins across the 20 samples (i.e. strides) for a given muscle. The resulting stride average for each muscle was a series of 120 bins that represented the average activity of that muscle during the stride. The stride averages facilitated comparison among dogs and trials by normalizing the duration of the strides.

Data of the different force manipulations were collected on separate days, necessitating a minimum of four recording days (i.e. added trunk mass, hills, added wrist mass, added horizontal force) for each subject. Separate control trials were collected each day and for each force manipulation. During the control trials, the dogs trotted unimpeded at the same speed as that of the corresponding force manipulation trials. Often control trials were collected both before and after the force manipulation. Analysis of successive control trials collected during a recording session provided an indication of whether or not the successive trials were influenced by muscle fatigue.

To illustrate the effects of the manipulations, the amplitude of EMGs was normalized to the average amplitude of the control trials. This normalization was performed in two steps. First, we calculated the average value for the 120 bins of the control trial. Then we divided each bin of the control and manipulation trials by this average control value. Once the data from each dog were normalized, we calculated average bin values for the six dogs for both the force manipulation and the control. By normalizing values for each dog prior to averaging across dogs, the pattern from one dog did not overwhelm the pattern from another (because of differences in EMG amplitude among electrodes, for example). These results were then displayed graphically (e.g. Fig. 2).

To determine whether or not a given force manipulation changed the recruitment of a given muscle we divided the total rectified, integrated area of the manipulation EMG by that of the control. If there was no effect of the manipulation, we would expect a ratio of 1. Thus, we tested for the effect of the

manipulation by comparing the mean ratio across dogs, using a one sample *t*-test with a hypothesized value of one. A fiducial limit for significance of $P < 0.05$ was chosen, and all results are presented as mean \pm 1 s.e.m.

To analyze the lateral and fore-aft pulling experiments, 35–40 strides were sampled in a given experimental manipulation (e.g. lateral pull to the left). The rectified integrated area of each EMG sample was determined by summing the data points in the sample. The mean force applied to the dog during each of the sampled strides was determined from the force transducer in series with the leash. The resulting 35–40 pairs of integrated EMG area (in mVs) and corresponding average forces (in N) were plotted against one another, with force as the independent variable, and the data were fitted using least-squares regression. The slope of the regression line was interpreted as the response of the dog to the increasing forces in terms of muscle recruitment. A slope was determined for every combination of muscle, dog, and experimental manipulation. The average slope from all dogs for each muscle in each manipulation was compared to a slope of zero (null hypothesis of no EMG response to the applied force). The hypothesis of a relationship between EMG area and pulling force (i.e. a slope different than zero) was rejected if the 95% confidence limits of the experimental slope encompassed zero. Statistical analyses were performed using StatView 5.0 and Microsoft Excel 2004 for Macintosh.

Results

In general, the force manipulations resulted in small or no changes in the periods of ipsilateral forelimb support and swing phases (Table 1). In the steep downhill trials (14°), we observed a 7% reduction in the period of the support phase, but no significant change in the period of the swing phase. In the added wrist mass trials, the duration of both support and swing phase were increased significantly. The swing phase of the 2% wrist mass trials was most dramatically effected, with a 26% increase in the period relative to the control trials. The only significant change we observed in the added anterior trunk mass trials was a 3% reduction in the period of the swing phase for the 8% added mass trials.

M. serratus ventralis thoracis

In trotting dogs, the slips of the serratus ventralis muscle inserting on the fifth and sixth ribs became active slightly before or coincidentally with the beginning of ipsilateral limb support (Fig. 2). Muscle activity rose rapidly during the initial portion of ipsilateral support and remained high for the first 40–50% of support. The muscle was silent during the last third of support and during swing phase.

The thoracic portion of the serratus ventralis muscle exhibited a significant increase in activity relative to the control, when 12% of body mass was added to the trunk in saddlebags in all four locations, anterior-trunk, mid-trunk, posterior-trunk, and split between the anterior and posterior-trunk sites (Table 2). The increased activity occurred during

Table 1. Mean values of support and swing phases of the ipsilateral forelimb for the force manipulations, presented as a proportion of the control values

	Mean change	P value
Uphill 10°		
Support phase	0.988	0.526
Swing phase	1.020	0.096
Uphill 14°		
Support phase	0.986	0.246
Swing phase	1.005	0.401
Downhill 10°		
Support phase	0.953	0.146
Swing phase	1.012	0.346
Downhill 14°		
Support phase	0.928	0.036*
Swing phase	0.991	0.357
Wrist mass 1%		
Support phase	1.093	0.0006*
Swing phase	1.110	0.011*
Wrist mass 2%		
Support phase	1.110	0.0015*
Swing phase	1.256	0.015*
Anterior trunk mass 8%		
Support phase	1.005	0.394
Swing phase	0.968	0.023*
Anterior trunk mass 12%		
Support phase	1.037	0.063
Swing phase	0.987	0.1136

*Value significantly different ($P < 0.05$).

Table 2. Mean response relative to control, standard error of change and significance of change from control of the m. serratus ventralis thoracis to the different force manipulations

Manipulation	N	Change (mean ± s.e.m.)	P value
Anterior-trunk mass			
8%	6	1.151±0.106	0.1063
12%	6	1.171±0.059	0.0173
Mid-trunk mass			
8%	6	1.205±0.085	0.0306
12%	6	1.306±0.044	0.0005
Posterior-trunk mass			
8%	6	1.131±0.059	0.0388
12%	6	1.301±0.073	0.0046
Anterior/posterior mass			
8%	6	1.115±0.078	0.1001
12%	6	1.330±0.134	0.0288
Hills			
Uphill 10°	6	1.132±0.119	0.1589
Uphill 14°	6	1.088±0.189	0.3301
Downhill 10°	6	1.327±0.180	0.0644
Downhill 14°	6	1.386±0.125	0.0138
Wrist mass			
1%	6	1.042±0.079	0.3065
2%	6	1.215±0.101	0.0433

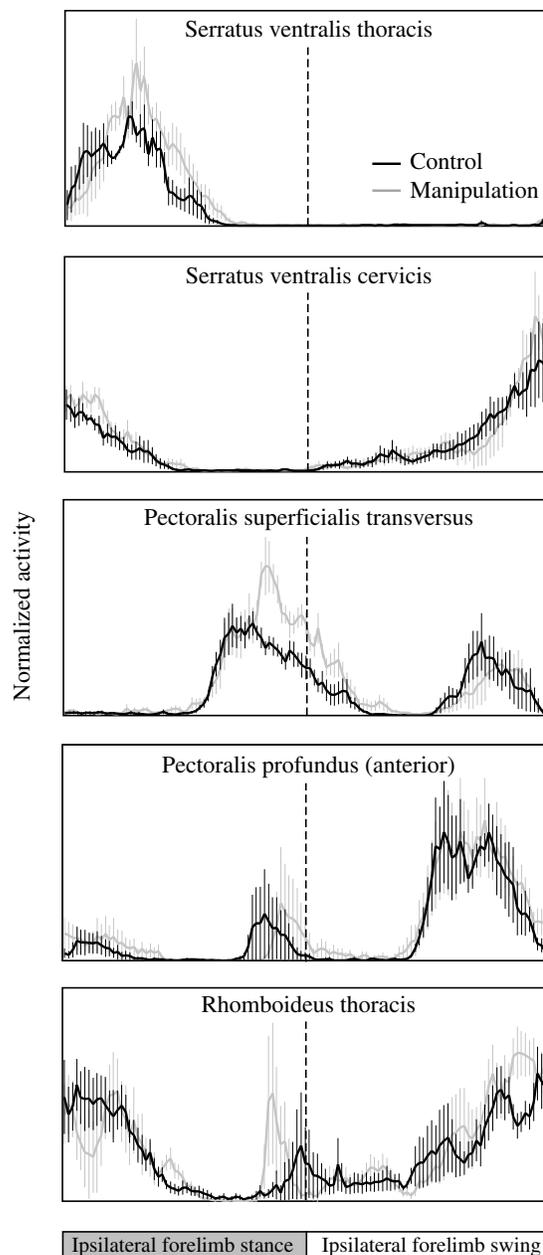


Fig. 2. Mean normalized EMGs from six dogs trotting with 12% of body mass carried in a backpack located over their pectoral girdle (i.e. anterior-trunk loading manipulation). For each muscle, the black line represents the average EMG when the dogs trotted on the level without added mass (control) and the grey line represents the average EMG when the dogs carried the added mass. For each dog, the trotting speed was the same during the control and added mass trials. The error bars are the s.e.m. for each sampling bin.

the normal trotting activity period of the muscle, specifically the first 60% of ipsilateral support (Fig. 2). A similar trend was observed in all four manipulations when 8% of body mass was added to the trunk, but the increase in activity was significantly different from the control values only in the mid-trunk and posterior-trunk manipulations.

This muscle also exhibited a significant increase in activity when the dogs trotted downhill, but not when they trotted uphill (Table 2). In the downhill trials, the muscle tended to become active prior to the beginning of ipsilateral support and activity was increased early in support and during the second half of support (Fig. 3). During trotting uphill, there was a decrease in activity early in support, followed by an increase in activity relative to the control at mid-stance. This initial decrease and mid-stance increase cancelled each other in the

analysis of integrated EMG area, resulting in no significant change from the control.

Application of horizontal forces to the dogs as they ran did not affect the activity of the thoracic portion of the serratus ventralis when the dogs resisted a forward pull, a right lateral pull and a left lateral pull (Table 3). There was, however, a significant negative relationship between the integrated muscle activity and the amplitude of the backward-directed force.

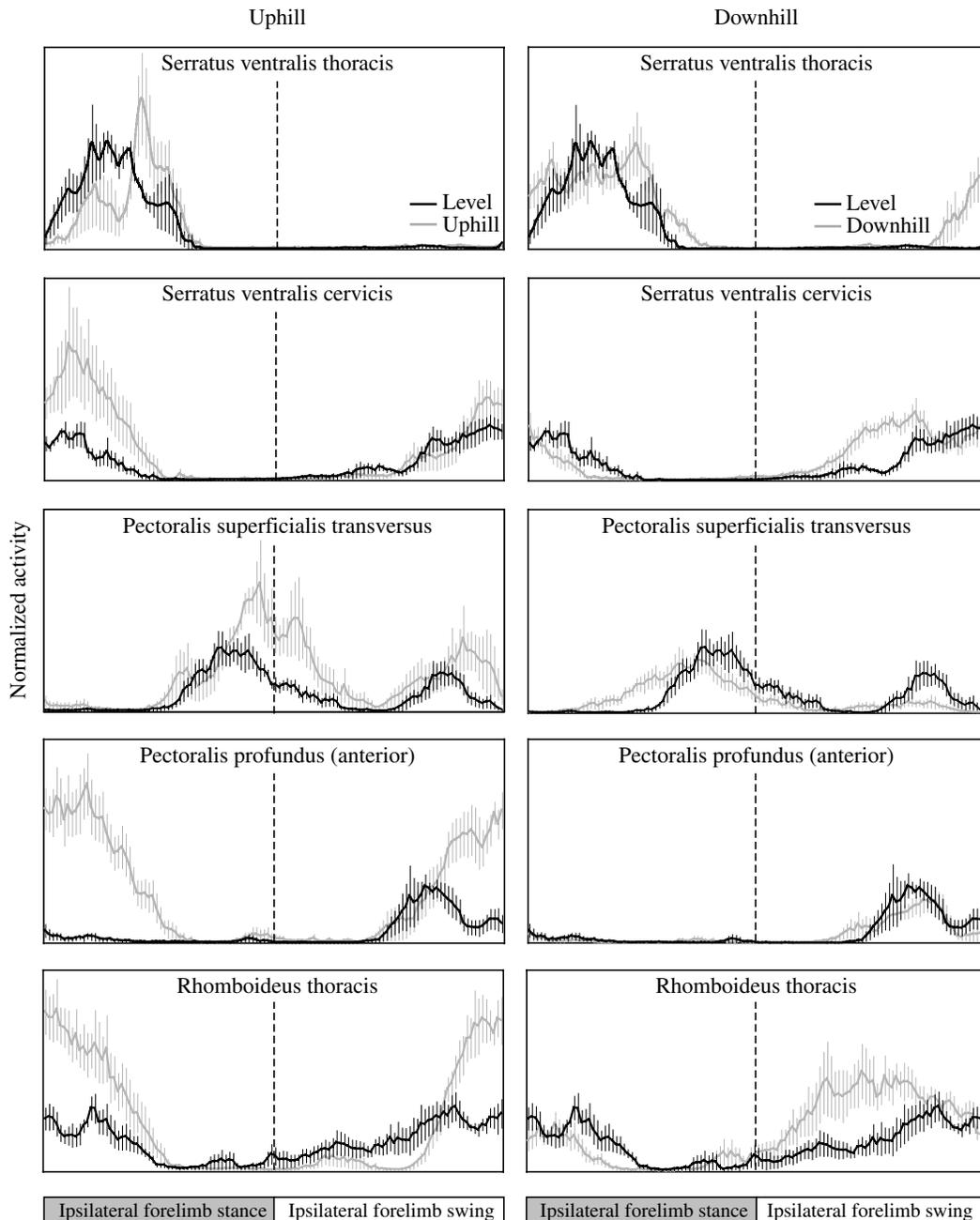


Fig. 3. Mean normalized EMGs from six dogs trotting uphill and downhill on an incline of 14° to the horizontal (i.e. fore-aft force manipulation). For each muscle, the black line represents the average EMG when the dogs trotted on the level (control) and the grey line represents the average EMG when the dogs trotted on the incline. For each dog, the trotting speed was the same during the control and incline trials. The error bars are the s.e.m. for each sampling bin.

Addition of mass to the wrists produced equivocal results. Adding 1% of body mass to each wrist did not result in a significant change in the total integrated activity, but adding 2% increased the activity (Table 2). The increase in activity occurred primarily at the end of swing phase and the initial part of support phase (Fig. 4).

M. serratus ventralis cervicis

During level trotting, activity of the cervical portion of the serratus ventralis muscle began during the swing phase of the ipsilateral leg (Fig. 2). The timing of the initial activity varied somewhat between dogs. Two of the dogs exhibited low levels of activity during the beginning of swing phase and the other four dogs initiated activity midway through swing phase. In all of the dogs, the muscle exhibited high levels of activity during the second half of ipsilateral swing and the first third of ipsilateral support.

Although there was a general trend toward increased activity when the dogs carried added mass on the trunk, only in the 8%

anterior-trunk and 8% girdle trials was the integrated activity significantly greater than the control values (Table 4). In no case was the integrated activity in the 12% increase trials found to be significantly elevated above control values.

Activity of the cervical portion of the serratus ventralis muscle increased when the dogs trotted, both uphill and downhill, relative to trotting on the level (Table 4). The increased activity, however, occurred during different phases of the stride cycle (Fig. 3). When the dogs ran uphill, the muscle exhibited increased activity during the normal trotting activity period of muscle; the beginning of ipsilateral limb support phase and, to a lesser extent, during the end of ipsilateral swing phase. In contrast, when they ran downhill, activity decreased during ipsilateral support and increased during the middle of ipsilateral swing.

Application of added horizontal force produced a significant relationship for only the forward-directed force (Table 3). Integrated muscle activity increased as the applied forward force increased.

Table 3. Results of horizontal force manipulations for the five muscles examined, showing the average slope, of all dogs, for EMG activity regressed against applied force

Muscle manipulation	N	Average slope	95% CI		Significance*
			Upper	Lower	
<i>Serratus ventralis thoracis</i>					
Rear pull	5	-0.000268	-0.00003	-0.000507	*
Front pull	5	0.000242	0.000529	-0.000045	NS
Left pull	5	0.000140	0.000287	-0.000007	NS
Right pull	5	0.000340	0.001217	-0.000530	NS
<i>Serratus ventralis cervicis</i>					
Rear pull	5	0.000162	0.000345	-0.000021	NS
Front pull	5	0.001000	0.001877	0.000124	*
Left pull	5	-0.000206	0.000029	-0.000441	NS
Right pull	5	-0.000016	0.000250	-0.000282	NS
<i>Pectoralis superficialis trans.</i>					
Rear pull	5	0.000447	0.000877	0.000017	*
Front pull	5	0.000020	0.000227	-0.000187	NS
Left pull	5	0.000166	0.000320	0.000013	*
Right pull	5	0.000166	0.000391	-0.000059	NS
<i>Pectoralis profundus ant.</i>					
Rear pull	5	0.001000	0.001877	0.000124	*
Front pull	5	0.000044	0.000135	-0.000047	NS
Left pull	5	-0.000036	0.000098	-0.000170	NS
Right pull	5	0.000268	0.000415	0.000121	*
<i>Rhomboideus</i>					
Rear pull	5	0.000138	0.000188	0.000088	*
Front pull	5	0.000162	0.000366	-0.000041	NS
Left pull	5	-0.000004	0.000104	-0.000113	NS
Right pull	5	-0.000061	0.00006	-0.000188	NS

CI, confidence intervals.

*Significant relationship between EMG activity and applied force, at the $P=0.05$ level, as indicated by the confidence intervals of the slope failing to encompass zero. NS, slope is not significantly different from zero.

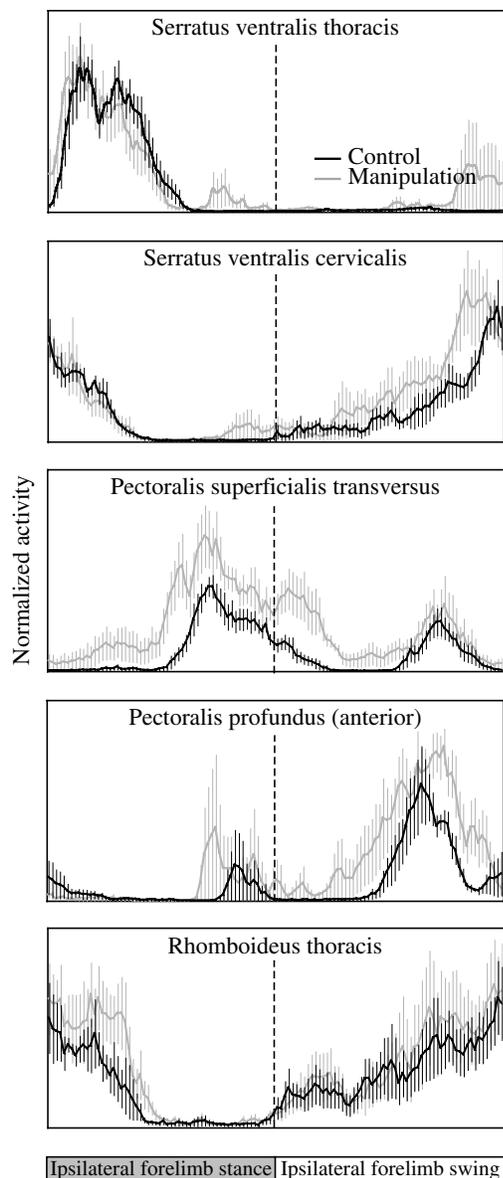


Fig. 4. Mean normalized EMGs from six dogs trotting with 2% of body mass added to each wrist (i.e. distal limb mass manipulation). For each muscle, the black line represents the average EMG when the dogs trotted on the level (control) and the grey line represents the average EMG when the dogs trotted with the added mass attached to the distal forelimbs. For each dog, the trotting speed was the same during the control and added mass trials. The error bars are the s.e.m. for each sampling bin.

The addition of mass to the wrists resulted in an increase of activity of the cervical portion of the serratus ventralis muscle (Table 4). This increase was most apparent during the end of ipsilateral swing phase (Fig. 4).

M. pectoralis superficialis transversus

The transverse portion of the superficial pectoralis muscle exhibited two distinct bursts of activity during level trotting

Table 4. Mean response relative to control, standard error of change, and significance of change from control of the *m. serratus ventralis cervicis* to the different force manipulations

Manipulation	<i>N</i>	Change (mean \pm s.e.m.)	<i>P</i> value
Anterior-trunk mass			
8%	6	1.230 \pm 0.079	0.0168
12%	6	1.110 \pm 0.073	0.0954
Mid-trunk mass			
8%	6	1.074 \pm 0.056	0.1238
12%	6	1.048 \pm 0.055	0.2092
Posterior-trunk mass			
8%	6	1.009 \pm 0.062	0.4467
12%	6	1.019 \pm 0.081	0.4100
Anterior/posterior mass			
8%	6	1.168 \pm 0.083	0.049
12%	6	1.053 \pm 0.053	0.1828
Hills			
Uphill 10°	6	1.496 \pm 0.246	0.0497
Uphill 14°	6	1.657 \pm 0.327	0.0503
Downhill 10°	6	1.433 \pm 0.191	0.0361
Downhill 14°	6	1.344 \pm 0.113	0.0144
Wrist mass			
1%	6	1.168 \pm 0.091	0.0621
2%	6	1.396 \pm 0.163	0.0298

(Fig. 2). The larger bursts was during the second half of ipsilateral limb support and the beginning of ipsilateral limb swing. The other burst was primarily associated with the second half of ipsilateral swing phase.

When mass was added to the trunk, we observed a significant change in the integrated activity in the 12% anterior-trunk trial but no change in activity in the other seven vertical loading trials (Table 5). The increased activity in the 12% trial occurred during the last 20% of ipsilateral support and the beginning of ipsilateral swing (Fig. 2). The activity during the second half of ipsilateral swing and the first two thirds of support was not influenced by addition of mass to the trunk.

When the dogs trotted uphill, activity of the transverse portion of the superficial pectoralis muscle increased during its normal period of activity (Fig. 3; Table 5). When the dogs trotted downhill, however, the muscle exhibited elevated activity in the middle of support but reduced activity during the end of swing phase (Fig. 3). The increased and decreased activity cancelled each other, such that there was no change in the total integrated area (Table 5).

Application of rearward-directed horizontal force resulted in an increase in the integrated muscle activity (Table 3). Increased activity was observed in both the end of support and the end of swing phase pulses. Leftward-directed horizontal forces also produced an increase in the activity (Table 3). In this case, the elevated activity was associated with the end of support pulse but not the end of swing pulse. Forward-directed and rightward-directed horizontal forces did not change the integrated activity.

Table 5. Mean response relative to control, standard error of change, and significance of change from control of the *m. pectoralis superficialis transversus* to the different force manipulations

Manipulation	N	Change (mean \pm s.e.m.)	P value
Anterior-trunk mass			
8%	6	1.133 \pm 0.125	0.1694
12%	6	1.188 \pm 0.064	0.0160
Mid-trunk mass			
8%	6	1.046 \pm 0.077	0.2875
12%	6	1.113 \pm 0.061	0.0626
Posterior-trunk mass			
8%	6	0.933 \pm 0.060	0.8426
12%	6	0.996 \pm 0.047	0.5339
Anterior/posterior mass			
8%	6	1.017 \pm 0.095	0.4333
12%	6	1.121 \pm 0.090	0.1182
Hills			
Uphill 10°	6	1.735 \pm 0.177	0.0044
Uphill 14°	6	2.061 \pm 0.227	0.0028
Downhill 10°	6	0.706 \pm 0.090	0.9889
Downhill 14°	6	0.921 \pm 0.076	0.8268
Wrist mass			
1%	6	1.495 \pm 0.243	0.0487
2%	6	2.009 \pm 0.322	0.0129

When mass was added to the wrists, activity of the transverse portion of the superficial pectoralis increased throughout the normal trotting activity period of the muscle (Fig. 4). The total integrated area of the activity was significantly elevated above the control values for both the 1% and 2% increase trials (Table 5).

Anterior region of the m. pectoralis profundus

During level trotting, activity of the anterior portion of the deep pectoralis muscle was primarily associated with the second half of ipsilateral swing phase, reaching peak amplitude at approximately 80% of the stride (Fig. 2). Two of the five dogs exhibited a second activity period, of much lower amplitude, during the first third of ipsilateral support phase. One of the five dogs exhibited a second activity period during the last third of ipsilateral support phase (Fig. 2).

Adding mass to the trunk did not alter the pattern or amplitude of the activity of the anterior aspect of the deep pectoralis muscle (Fig. 2). This was true for all trunk loading manipulations (Table 6).

When the dogs trotted uphill, activity of the anterior part of the deep pectoralis increased during the last third of ipsilateral swing phase and the first half of ipsilateral support phase (Fig. 3; Table 6). The greatest increase in activity was associated with the first 40% of the support phase, a period during which this muscle exhibited very low or no activity when the dogs trotted at constant speed on the level. Running downhill had no effect on the activity of this portion of the deep pectoralis.

Application of horizontal forces to the trotting dogs

Table 6. Mean response relative to control, standard error of change, and significance of change from control of the *m. pectoralis profundus* (anterior) to the different force manipulations

Manipulation	N	Change (mean \pm s.e.m.)	P value
Anterior-trunk mass			
8%	5	1.193 \pm 0.140	0.1136
12%	5	1.165 \pm 0.145	0.1529
Mid-trunk mass			
8%	5	1.092 \pm 0.106	0.2179
12%	5	1.343 \pm 0.228	0.1031
Posterior-trunk mass			
8%	5	0.911 \pm 0.085	0.8223
12%	5	1.166 \pm 0.140	0.1511
Anterior/posterior mass			
8%	5	0.917 \pm 0.051	0.9086
12%	5	0.996 \pm 0.084	0.5162
Hills			
Uphill 10°	5	3.392 \pm 0.508	0.0046
Uphill 14°	5	4.915 \pm 0.755	0.0033
Downhill 10°	5	0.735 \pm 0.153	0.9211
Downhill 14°	5	0.824 \pm 0.182	0.8060
Wrist mass			
1%	5	1.502 \pm 0.135	0.0104
2%	5	2.048 \pm 0.116	0.0004

produced a positive relationship for both the rearward- and rightward-directed forces (Table 3). Rearward-directed forces resulted in increased activity during both the end of swing phase and the first half of support phase, a pattern that was very similar to that observed during trotting uphill. Rightward-directed horizontal forces also increased the activity during both the end of swing and the first half of support phase.

Adding mass to the wrist resulted in an increase of activity in the anterior portion of the deep pectoralis during the last two-thirds of ipsilateral swing phase, the normal trotting activity period (Fig. 4; Table 6). The apparent increase in activity during the last part of support was not significant. Activity during the first portion of the support phase was not changed by the addition of mass to the wrists.

M. rhomboideus thoracis

The activity period of the thoracic portion of the rhomboideus muscle varied somewhat from dog to dog. In all six dogs the muscle was active during the second half of ipsilateral swing phase and the first half of ipsilateral support phase (Fig. 2). Two of the dogs also exhibited a burst of activity during the beginning of ipsilateral swing phase.

Adding mass to the trunk did not change the activity of the thoracic portion of the rhomboideus muscle during trotting (Fig. 2; Table 7). None of the eight manipulations in which mass was added to the trunk resulted in a significant change in the total integrated EMG activity.

When the dogs trotted uphill, activity of the thoracic portion of the rhomboideus muscle increased dramatically during the normal trotting activity period; the last third of ipsilateral

Table 7. Mean change in integrated electromyogram relative to control, standard error of change, and significance of change from control of the *m. rhomboideus* to the different force manipulations

Manipulation	<i>N</i>	Change (mean ± s.e.m.)	<i>P</i> value
Anterior-trunk mass			
8%	6	0.934±0.102	0.7287
12%	6	1.062±0.059	0.171
Mid-trunk mass			
8%	6	0.761±0.135	0.9318
12%	6	0.830±0.165	0.8243
Posterior-trunk mass			
8%	6	0.858±0.155	0.7999
12%	6	0.889±0.148	0.7561
Anterior/posterior mass			
8%	6	0.822±0.078	0.9645
12%	6	1.013±0.158	0.4696
Hills			
Uphill 10°	6	1.373±0.135	0.02
Uphill 14°	6	1.716±0.204	0.0086
Downhill 10°	6	1.266±0.116	0.0352
Downhill 14°	6	1.456±0.211	0.0416
Wrist mass			
1%	6	1.284±0.092	0.0136
2%	6	1.309±0.103	0.0148

swing and the first half of ipsilateral support (Fig. 3; Table 7). When the dogs ran downhill, activity increased during the middle of ipsilateral swing and decreased during the first half of ipsilateral support (Fig. 3; Table 7).

Application of rearward-directed horizontal forces to the dogs as they ran increased the activity of the thoracic portion of the rhomboideus muscle (Table 3). This increase occurred during normal trotting activity period. Forward-, right lateral-, or left lateral-directed horizontal forces, however, did not influence activity of this muscle.

Addition of mass to the wrists, produced an increase in the activity of the thoracic portion of the rhomboideus muscle during its normal period of activity; the last-half to last-third of ipsilateral swing and the first-half of ipsilateral support (Fig. 4; Table 7). The most consistent increase in activity occurred during the first half of support phase.

Discussion

Interpretations of the locomotor function of the extrinsic muscles of the forelimb of mammals have relied primarily on the musculoskeletal anatomy of the shoulder (Davis, 1949; Gray, 1968) and on three studies that have described the recruitment patterns of the muscles in Virginia opossums (Jenkins and Weijs, 1979), domestic cats (English, 1978) and domestic dogs (Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974). Additionally, activity of the serratus ventralis thoracis during walking has been documented in vervet monkeys (Schmitt et al., 1994), and activity of the serratus ventralis and pectoralis muscles during flight have been described in the bats

Artibeus jamaicensis (Hermanson and Altenbach, 1985) and *Antrozous pallidus* (Hermanson and Altenbach, 1983). A recent study used estimates of maximum isometric force and maximum power based on measurement of physiological cross-sectional area and contraction velocity data to infer the function of the extrinsic muscles of the forelimb of horses (Payne et al., 2005).

Locomotor function of the 'muscular sling'

M. serratus ventralis thoracis

The thoracic portion of the serratus ventralis muscle exhibited a pattern of activity during level trotting and responded to the force manipulations in a manner that is consistent with the function of supporting body weight during running. During level trotting the muscle was active during the first half of ipsilateral limb support and displayed no activity during the swing phase of the ipsilateral limb. When mass was added to the trunk, recruitment of the muscle increased during this same period in the locomotor cycle, suggesting that the muscle is recruited to resist gravity. The increased activity in response to running downhill also suggested a role in vertical support, because running downhill requires quadrupedal animals to support more of their body weight with their forelimbs than when they run on the level. By contrast, when the dogs ran uphill recruitment of the thoracic serratus ventralis decreased during the initial portion of limb support, but increased during mid-support, resulting in no net change. Thus, the recruitment patterns during running on hills were also consistent with the function of supporting body weight. The increased activity when the dogs ran with 2% of body mass strapped to their wrists suggests that the thoracic serratus ventralis may have a capacity to assist limb retraction when the limb is fully protracted. Nevertheless, the negative relationship between muscle activity and horizontal force when the dogs resisted backward-directed forces suggests that this muscle does not contribute to limb retraction during stance. The decline in muscle activity in response to the application of rearward-directed force may have been due to an unweighting of the forelimbs. In summary, the results from the different force manipulations indicate that the thoracic portion of the serratus ventralis muscle functions primarily to support body weight in trotting dogs.

M. serratus ventralis cervicis

The results of the force manipulations suggest that the cervical portion of the serratus ventralis does not function in support of body weight. Rather, it appears to define the fulcrum of the forelimb in the cranial-caudal direction during active forelimb retraction. The fulcrum of the forelimb, which is located near the dorsal edge of the scapula (Gray, 1968; Fisher, 1994; Fisher et al., 2002), must be stabilized against caudal displacement when muscles such as the latissimus dorsi actively retract the forelimb. The cervical slips of the serratus ventralis could provide this stabilization of the fulcrum because they pass caudally from the transverse processes of the cervical vertebrae to attach on the dorsal,

medial surface of the scapula. Several observations are consistent with this interpretation.

During level trotting, the cervical portion of the serratus ventralis muscle was active during the end of swing phase and the beginning of support phase. Adding mass to the trunk did not consistently increase recruitment of the muscle (Table 4), suggesting the muscle is not associated with supporting the body against gravity. When the dogs ran downhill, recruitment increased during the swing phase, but decreased during support phase. This result is also inconsistent with the function of resisting gravity. The results of downhill running are consistent, however, with an increased demand for limb retraction during the end of swing phase and a reduced demand for limb retraction during limb support. The dramatically increased recruitment of this muscle during the first half of limb support when the dogs ran uphill is consistent with the suggestion that this muscle functions primarily to anchor the fulcrum of the forelimb during active retraction of the limb. When mass was added to the wrists, recruitment of the cervical portion of the serratus ventralis increased during the end of ipsilateral swing phase. In this case, also, the result is consistent with the cervical portion of the serratus ventralis functioning not in the support of body mass, but to stabilize the fulcrum during forelimb retraction. The one result that was not consistent with a role in limb retraction was the lack of an increase in muscle activity when rearward-directed horizontal forces were applied to the subjects (Table 3). This suggests that our interpretation is incorrect or that the application of rearward-directed forces had unanticipated effects on the subjects, such as unloading the forelimb so that it was less able to contribute to propulsion. The increase in integrated muscle activity in response to applied forward-directed force was due to an increase in recruitment during the second half of swing phase. This is consistent with a more rapid retraction of the limb at the end of swing phase. Recruitment during support decreased with the application of forward forces. In summary, the cervical portion of the serratus ventralis muscle does not appear to contribute to vertical support of the body during trotting in dogs. With the exception of the lack of an increase in muscle activity when we applied rearward-directed horizontal force to the subjects, the results of the various force manipulations suggest that this muscle functions primarily to anchor the fulcrum of the forelimb (i.e. dorsal aspect of the scapula) in the cranial-caudal direction during active retraction of the forelimb.

M. pectoralis superficialis transversus

During normal trotting on level surfaces, this muscle exhibited two bursts of activity, one associated with the end of ipsilateral support phase and the beginning of swing phase, and the other associated with the end of ipsilateral swing phase. When the dogs ran with mass added to their trunk an increase in muscle recruitment was observed in the 12% anterior-trunk trial, but none of the other vertical load trials. The increased activity in this trial was associated with the last 15% of support and the beginning of swing phase. The observation that the

increased activity was associated with the very end of stance phase suggests that the transverse pectoralis is not involved in support of body weight. When the dogs ran downhill, activity associated with mid-stance increased and that associated with swing phase decreased. The increased activity in the middle of support is consistent with a role in support of body weight at the end of stance when dogs run downhill. However, a corresponding decrease in recruitment at this phase of the locomotor cycle when the dogs ran uphill, as would be expected if the muscle functioned in vertical support, was not observed. Instead, when the dogs ran uphill recruitment increased significantly during the transition period from ipsilateral support to swing phase and at the end of swing phase (i.e. the period during which the muscle is active during level trotting). When the dogs trotted with mass added to their wrists, activity was elevated throughout the normal activity period for level trotting. This result and the response of the muscle to both uphill running and added mass on the trunk suggest that the transverse portion of the superficial pectoralis functions primarily in applying protraction/retraction torques to the limb. The anatomical configuration of the muscle, extending roughly transversely from the sternum to the proximal humerus and its biphasic activity pattern raises the possibility that the transverse pectoralis can function as both a protractor and a retractor of the limb, depending on position of the limb. At the end of ipsilateral support phase, when the shoulder is rotated caudally and protraction of the limb in swing phase must begin, the transverse pectoralis probably has an orientation that can assist protraction of the limb. Then, at the end of swing phase, when the shoulder is extended cranially, the orientation of the transverse pectoralis may allow it to assist in retraction of the limb. Additionally, the increased activity during the last quarter of ipsilateral support in 12% anterior-trunk trials and the increased activity during the middle of support in the downhill trials are consistent with a role in the support of body weight for this portion of the pectoralis muscle when there is a net retracting moment imposed on the shoulder.

Anterior region of the m. pectoralis profundus

The anterior portion of the deep pectoralis appears to function primarily in retraction of the limb. In level trotting, this portion of the pectoralis is active during the second half of ipsilateral swing phase, exhibiting little or no activity during the support phase. Although its orientation, extending laterally and dorsally from the sternum to the proximal humerus, would allow it to assist in support of body weight, the addition of mass to the trunk during trotting did not produce a significant increase in its recruitment. The lack of increased activity in this muscle when the dogs ran downhill also suggests that it does not contribute to support of body weight. The dramatically increased recruitment during the beginning of support both when the dogs ran uphill and when rearward-directed horizontal were applied suggest that this muscle assists in retraction of the limb. The increased activity during the normal trotting activity period when mass was added to the wrists is

also consistent with the muscle acting as a retractor of the limb. Thus, during trotting on level surfaces, this portion of the deep pectoralis contributes to limb retraction during the end of swing phase, but appears not to be involved in limb retraction during support. When dogs run uphill or resist rearward-directed horizontal forces, however, this portion of the deep pectoralis retracts the forelimb to propel the dog forward.

M. rhomboideus thoracis

The observation that integrated EMG area did not increase when we added mass to the trunk of trotting dogs suggests that the thoracic portion of the rhomboideus muscle does not contribute to vertical support of the body during running. The most dramatic response we obtained from this muscle occurred when the dogs ran uphill. In this case, the activity associated with the end of swing phase and the first half of ipsilateral support increased substantially. This result suggests that the rhomboideus muscle functions to stabilize the fulcrum of the forelimb during active retraction of the forelimb, in a manner similar to what we have suggested for the cervical portion of the serratus ventralis. The results from the applied horizontal force experiments are also consistent with this interpretation. We observed a significant increase in activity when the trotting dogs resisted a rearward-directed horizontal force, but not when forward-, right-, or left-directed horizontal forces were applied. Although it is not dramatically illustrated in Fig. 4, the response of this muscle to the added wrist mass was also consistent with the function of limb retraction. In summary, these results suggest that the thoracic portion of the rhomboideus muscle functions to stabilize the fulcrum of the forelimb during active retraction of the forelimb and does not appear to support body mass during trotting in dogs.

Organization and function of the therian shoulder

In therian mammals, support of body weight at the pectoral girdle is accomplished by two sets of muscles. First, muscles that act as protractors or retractors of the forelimb support the body against gravity by preventing collapse at the shoulder. As explained above, the function of forelimb protractors and retractors in support of body weight is dependent on the polarity and amplitude of the moment at the fulcrum of the scapula on the trunk. Second, the high mobility of the shoulder in therian mammals requires muscles with a vertical fascicle orientation to provide a linkage between the forelimb and trunk. This linkage in conjunction with the extrinsic retractor and protractor muscles determines the location of the fulcrum that transmits gravitational and locomotor forces between the forelimb and trunk. The set of muscles that have attachment sites and fiber orientations appropriate for the transfer of vertically oriented forces are generally referred to as the 'muscular sling' (Fig. 1).

The observations of this study suggest that only one element of the muscular sling, the thoracic portion of the serratus ventralis (*m. serratus ventralis thoracis*), functions in the support of body weight during level trotting in dogs. The other muscles of the sling (*m. serratus ventralis cervicis*, anterior

elements of the pectoralis complex, and *m. rhomboideus thoracis*) function in retraction and/or protraction of the forelimb and do not appear to assist in support of body weight during level trotting. The finding that support against gravity in dogs is provided primarily by the thoracic portion of the serratus ventralis muscle is consistent with anatomical observations in horses that suggest the serratus ventralis thoracis differs from the other extrinsic muscles of the forelimb in having a high capacity to generate force and resist gravity (Payne et al., 2005). The result is also consistent with the observation that the fulcrum of the forelimb during trotting in therian mammals is located in the same region of the dorsal scapula as the serratus ventralis inserts (Gray, 1968; Fischer, 1994; Fischer et al., 2002).

The result that adding mass to the trunk did not increase the activity of muscles functioning to stabilize the fulcrum of the forelimb during active retraction of the forelimb, such as the *m. serratus ventralis cervicis* and *m. rhomboideus thoracis*, seems paradoxical. If there is a net retraction moment on the forelimb, adding mass to the trunk would, in most instances, increase that moment and elicit an increase in the muscles that are responsible for the moment. We suspect that the explanation is that the ground reaction force vector is oriented so that it passes through, or very near, the fulcrum of the shoulder, such that there is little or no moment at the shoulder during level trotting. This would also explain the lack of muscle activity during ipsilateral support from the major forelimb retractors, the *m. latissimus dorsi* and posterior portion of the *m. pectoralis profundus*, when dogs trot on level surfaces (Tokuriki, 1973b) (D. R. Carrier, unpublished observations). If, in fact, there is little or no moment at the shoulder during level trotting in dogs, the observed activity of the *m. serratus ventralis cervicis* and *m. rhomboideus thoracis* during the beginning of ipsilateral support (e.g. Fig. 3) may be associated with stabilization of the scapula in the parasagittal plane rather than with the production of a moment at the shoulder. In any case, the results of this study suggest that when dogs trot on level surfaces: (1) the *m. serratus ventralis thoracis* is solely responsible for support of body weight at the pectoral girdle, (2) the ground reaction force vector is oriented at the fulcrum of the shoulder such that the forelimb functions as a strut (Gray, 1968) and there is little or no retraction/protraction moment at the shoulder.

Reducing the moment at the shoulder when running at constant speed could be expected in a species specialized for sustained running for at least two reasons. First, if the forelimb behaved as a strut at its attachment to the trunk, the work of running would be accomplished not by the extrinsic muscles, but by the muscles of the more distal joints. Comparisons of the negative and positive work done at individual joints during a running step (Alexander and Vernon, 1975; Alexander, 1984; Gregersen et al., 1998), analyses of the mechanical properties and dimensions of tendons (Dimery and Alexander, 1985; Ker et al., 1988) and measurements of muscle and/or tendon strain (Roberts et al., 1997; Carrier et al., 1998; Biewener et al., 1998; Gillis and Biewener, 2001; Daley and Biewener, 2003;

Biewener et al., 2004) all indicate that it is the extensor muscles of the distal joints that are most suitable for the storage and recovery of elastic strain energy. Thus, limiting the moment at the fulcrum of the shoulder during constant-speed running would result in a reduction in the cost of transport by making full use of elastic storage at the distal joints during a running step, while minimizing the work done at the shoulder. Second, if the moments at the shoulder are minimized, locomotor forces imposed on the trunk by the extrinsic forelimb muscles will be also be minimized. Reducing locomotor loading of the trunk can be expected to facilitate costal ventilation of the lungs, by reducing potential conflicts between the locomotor and ventilatory functions of individual hypaxial muscles or groups of hypaxial muscles (Carrier, 1987; Owerkowicz et al., 1999; Deban and Carrier, 2002).

Based on musculo-skeletal architecture, Davis and Gray (Davis, 1949; Gray, 1968) proposed that the m. serratus ventralis muscle is primarily or wholly responsible for vertical support of the body at the forelimbs in mammals. In addition to our results, data from Virginia opossums and domestic cats are consistent with the m. serratus ventralis functioning in vertical support. In opossums (*Didelphis virginiana*) ambulating at 0.95 m s^{-1} (Jenkins and Weijs, 1979) and cats trotting (English, 1978) the cervical and thoracic parts of the serratus ventralis are active during the middle of ipsilateral support. However, as Jenkins and Weijs point out, the activity patterns of the pectoralis and rhomboideus muscles in both opossums and cats are also consistent with a role in vertical support of the body (Jenkins and Weijs, 1979). Thus, additional work is needed to determine the function of the different components of the muscular sling and to find out whether or not the observations of this study are widespread among therian mammals or are unique to dogs.

Summary and conclusions

Our manipulations of locomotor forces suggest that the thoracic portion of the serratus ventral muscle is primarily or entirely responsible for support of body weight at the pectoral girdle during trotting in dogs. Its activity increased when we added mass to the subjects' trunk and when we ran the subjects downhill. Its activity decreased when we applied a rearward-directed force to subjects, presumably because of an unloading of the forelimbs. The m. serratus ventralis thoracis exhibited little or no response to the other force manipulations. In contrast, the cervical portion of the serratus ventralis did not show a consistent increase in activity in response to added mass. When the dogs ran downhill, recruitment increased during the swing phase, but decreased during support phase. Its activity, however, did increase significantly when we ran the subjects uphill and added mass to their wrists. Thus, the results of the various force manipulations suggest that m. serratus ventralis cervicis muscle functions primarily to stabilize the fulcrum of the forelimb in the cranial-caudal direction during active retraction of the forelimb.

The m. pectoralis superficialis transversus is unique among the muscles of the muscular sling because it appears to

contribute to both protraction and retraction of the forelimb, depending on the position of the limb. In contrast, the anterior portion of the pectoralis profundus appears to function primarily as a retractor of the forelimb during both the end of swing phase and during the beginning of ipsilateral support phase. The thoracic portion of the rhomboideus muscle appears to stabilize the fulcrum of the forelimb in the cranial-caudal direction during active retraction of the forelimb.

The result that adding mass to the trunk did not increase the activity of muscles associated with forelimb retraction, such as the m. serratus ventralis cervicis and m. rhomboideus thoracis, suggests that the ground reaction force vector is oriented so that it passes through, or very near, the fulcrum of the shoulder, such that there is little or no moment at the shoulder during level trotting. This may represent specialization that reduces the cost of running at constant speed and reduces locomotor loads on the axial musculo-skeletal system in a way that facilitates simultaneous running and breathing.

We wish to thank Eric Stakebake, Jessamyn Markley and Nadja Schilling for assisting with surgery and/or collection of data. These individuals, plus Farish Jenkins, David Lee, Rebecca Walter and an anonymous reviewer, read the manuscript and provided very helpful feedback. This research was supported by NSF grant IBN-0212141.

References

- Alexander, R. McN. (1984). Elastic energy stores in running vertebrates. *Am. Zool.* **24**, 85-94.
- Alexander, R. McN. and Vernon, A. (1975). The mechanics of hopping by kangaroos (Macropodidae). *J. Zool., Lond.* **177**, 265-303.
- Banzett, R. B., Mead, J., Reid, M. B. and Topulos, G. P. (1992a). Locomotion in men has no appreciable mechanical effect on breathing. *J. Appl. Physiol.* **72**, 1922-1926.
- Banzett, R. B., Nations, C. S., Wang, N., Butler, J. P. and Lehr, J. L. (1992b). Mechanical independence of wingbeat and breathing in starlings. *Respir. Physiol.* **89**, 27-36.
- Basmajian, J. V. and Stecko, G. A. (1962). A new bipolar indwelling electrode for electromyography. *J. Appl. Physiol.* **17**, 849.
- Biewener, A. A., Konieczynski, D. D. and Baudinette, R. V. (1998). *In vivo* muscle force-length behavior during steady-state hopping in tammar wallabies. *J. Exp. Biol.* **201**, 547-565.
- Biewener, A. A., McGowan, C., Card, G. M. and Baudinette, R. V. (2004). Dynamics of leg muscle function in tammar wallabies (*M. eugenii*) during level versus incline hopping. *J. Exp. Biol.* **207**, 211-223.
- Carrier, D. R. (1987). The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. *Paleobiology* **13**, 326-341.
- Carrier, D. R., Gregersen, C. S. and Silverton, N. A. (1998). Dynamic gearing in running dogs. *J. Exp. Biol.* **201**, 3185-3195.
- Daley, M. A. and Biewener, A. A. (2003). Muscle force-length dynamics during level versus incline locomotion: a comparison of *in vivo* performance of two guinea fowl ankle extensors. *J. Exp. Biol.* **206**, 2941-2958.
- Davis, D. D. (1949). The shoulder architecture of bears and other carnivores. *Fieldiana (Zool.)* **31**, 285-305.
- Deban, S. M. and D. R. Carrier. (2002). Hypaxial muscle activity during running and breathing in dogs. *J. Exp. Biol.* **205**, 1953-1967.
- 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.
- English, A. W. (1978). Functional analysis of the shoulder girdle of cats during locomotion. *J. Morph.* **156**, 279-292.
- Evans, H. E. (1993). *Miller's Anatomy of the Dog*. Philadelphia: W. B. Saunders Company.
- Fischer, M. S. (1994). Crouched posture and high fulcrum. A principle in the locomotion of small mammals: the example of the rock hyrax (*Procapra capensis*) (Mammalia: Hyracoidea). *J. Human Evol.* **26**, 501-524.

- Fischer, M. S., Schilling, N., Schmidt, M., Haarhaus, D. and Witte, H. F.** (2002). Basic limb kinematics of small therian mammals. *J. Exp. Biol.* **205**, 1315-1338.
- Gillis, G. B. and Biewener, A. A.** (2001). Hindlimb muscle function in relation to speed and gait: *in vivo* patterns of strain and activation in a hip and knee extensor of the rat (*Rattus norvegicus*). *J. Exp. Biol.* **204**, 2717-2731.
- Gray, J.** (1968). *Animal Locomotion*. London: Weidenfeld and Nicolson.
- Gregersen, C. S., Silverton, N. A. and Carrier, D. R.** (1998). External work and potential for elastic storage at the limb joints of running dogs. *J. Exp. Biol.* **201**, 3197-3210.
- Hermanson, J. W. and Altenbach, J. S.** (1983). The functional anatomy of the shoulder of the Pallid bat, *Antrozous pallidus*. *J. Mammal.* **64**, 62-74.
- Hermanson, J. W. and Altenbach, J. S.** (1985). Functional anatomy of the shoulder and arm of the fruit-eating bat *Artibeus jamaicensis*. *J. Zool., Lond.* **205**, 157-177.
- Jenkins, F. A. and Weijjs, W. A.** (1979). The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). *J. Zool., Lond.* **188**, 379-410.
- Kardong, K. V.** (1998). *Vertebrates – Comparative Anatomy, Function, Evolution*. Boston: McGraw-Hill.
- Ker, R. F., Alexander, R. McN. and Bennett, M. B.** (1988). Why are mammalian tendons so thick? *J. Zool. Lond.* **216**, 309-324.
- Owerkowicz, T., Farmer, C., Hicks, J. W. and Brainerd, E. L.** (1999). Contribution of gular pumping to lung ventilation in monitor lizards. *Science* **284**, 1661-1663.
- Payne, R. C., Veenman, P. and Wilson, A. M.** (2005). The role of the extrinsic thoracic limb muscles in equine locomotion. *J. Anat.* **206**, 193-204.
- 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.
- Romer, A. S.** (1956). *Osteology of the Reptiles*. Chicago: The University of Chicago Press.
- Schmitt, D., Larson, S. G. and Stern, J. T. J.** (1994). Serratus ventralis function in vervet monkeys (*Cercopithecus aethiops*): are primate quadrupeds unique? *J. Zool. Lond.* **232**, 215-230.
- Tokuriki, M.** (1973a). Electromyographic and joint-mechanical studies in quadrupedal locomotion. I. Walk. *Jpn. J. vet. Sci.* **35**, 433-446.
- Tokuriki, M.** (1973b). Electromyographic and joint-mechanical studies in quadrupedal locomotion. II. Trot. *Jpn. J. vet. Sci.* **35**, 525-533.
- Tokuriki, M.** (1974). Electromyographic and joint-mechanical studies in quadrupedal locomotion. III. Gallop. *Jpn. J. vet. Sci.* **36**, 121-132.