Locomotor function of forelimb protractor and retractor muscles of dogs: evidence of strut-like behavior at the shoulder

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SUMMARY

The limbs of running mammals are thought to function as inverted struts. When mammals run at constant speed, the ground reaction force vector appears to be directed near the point of rotation of the limb on the body such that there is little or no moment at the joint. If this is true, little or no external work is done at the proximal joints during constant-speed running. This possibility has important implications to the energetics of running and to the coupling of lung ventilation to the locomotor cycle. To test if the forelimb functions as an inverted strut at the shoulder during constant-speed running and to characterize the locomotor function of extrinsic muscles of the forelimb, we monitored changes in the recruitment of six muscles that span the shoulder (the m. pectoralis superficialis descendens, m. pectoralis profundus, m. latissimus dorsi, m. omotransversarius, m. cleidobrachialis and m. trapezius) to controlled manipulations of locomotor forces and moments in trotting dogs (*Canis lupus familiaris* Linnaeus 1753). Muscle activity was monitored while the dogs trotted at moderate speed (approximately 2 m s⁻¹) on a motorized treadmill. Locomotor forces were modified by (1) adding mass to the trunk, (2) inclining the treadmill so that the dogs ran up- and downhill (3) adding mass to the wrists or (4) applying horizontally directed force to the trunk through a leash. When the dogs trotted at constant speed on a level treadmill, the primary protractor muscles of the forelimb exhibited activity during the last part of the ipsilateral support phase and the beginning of swing phase, a pattern that is consistent with the initiation of swing phase but not with active protraction of the limb during the beginning of support phase. Results of the force manipulations were also consistent with the protractor muscles initiating swing phase and contributing to active braking *via* production of a protractor moment on the forelimb when the dogs decelerate. A similar situation appears to be true for the major retractor muscles of the forelimb. The m. pectoralis profundus and the m. latissimus dorsi were completely silent during the support phase of the ipsilateral limb when the dogs ran unencumbered and exhibited little or no increase in activity when the dogs carried added mass on their backs to increase any retraction torque during the support phase of constant-speed running. The most likely explanation for these observations is that the ground force reaction vector is oriented very close to the fulcrum of the forelimb such that the forelimb functions as a compliant strut at the shoulder when dogs trot at constant speed on level surfaces. Because the moments at the fulcrum of the pectoral girdle appear to be small during the support phase of a trotting step, a case can be made that it is the activity of the extrinsic appendicular muscles that produce the swing phase of the forelimb that explain the coupled phase relationship between ventilatory airflow and the locomotor cycle in trotting dogs.

Key words: forelimb, retractor muscles, protractor muscles, EMG, recruitment, quadruped, running, shoulder.

INTRODUCTION

A well-supported model of terrestrial locomotion envisions limbs functioning as spring-loaded inverted struts (Gray, 1944; Gray, 1968; Alexander, 1984; Blickhan, 1989; Blickhan and Full, 1993). During running at constant speed on level surfaces, the ground reaction force vector is thought to be directed more or less through the point of rotation of the limb on the body such that there is little or no moment at the joint and, therefore, little or no external work done at the proximal joints during a running step (Winter, 1983; Carrier et al., 1998; Roberts and Belliveau, 2005). Instead, the muscles that extend the distal limb joints appear to produce the external work of the step. These distal muscles are thought to contract isometrically and, together with their in-series tendons, to function as springs to store and recover elastic strain energy during the support phase of a running step (Cavagna et al., 1964; Cavagna et al., 1977; Alexander, 1984; Roberts et al., 1997). In this way, the cost of locomotion is greatly reduced.

Support for the elastic storage portion of this hypothesis of limb function is solid. Early comparisons of the mechanical work and oxygen consumption of running humans and hopping kangaroos indicated that as much as 50% of the energy needed for locomotion may be saved by elastic storage in running animals (Cavagna et al., 1964; Alexander and Vernon, 1975; Cavagna et al., 1977). 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 (Ker et al., 1986; Ker et al., 1988) and measurements of muscle and/or tendon strain (Roberts et al., 1997; Carrier et al., 1998; Biewener et al., 1998b; Biewener, 1998; Gillis and Biewener, 2001; Daley and Biewener, 2003) all indicate that it is the extensor muscles and tendons of the distal joints that are most suitable for the storage and recovery of elastic strain energy.

Evidence supporting a strut-like action of the limb at the proximal joint during constant-speed running (Gray, 1944; Gray,

1968), however, is not as strong. If the ground reaction force vector points directly at the fulcrum of the limb on the trunk then the protractor and retractor muscles of the limb will not need to be active during the support phase of the step. This possibility is supported by several studies reporting that the ground reaction force vector is directed at the hip joint during a running step in humans (Roberts and Belliveau, 2005) and during mid-stance in running dogs (Carrier et al., 1998). Nevertheless, recordings of activity of the limb muscles that extend from the trunk to the limb (i.e. extrinsic appendicular muscles) during running provide conflicting observations. Several studies have found that the major retractor muscles of the forelimb (pectoralis profundus and latissimus dorsi) are active during the support phase of running steps in Virginia opossums (Jenkins and Weijs, 1979), dogs (Tokuriki, 1973; Goslow et al., 1981) and cats (English, 1978), suggesting that the forelimb does not function as a strut during constant-speed running. The strut hypothesis is supported, however, by electromyograms (EMGs) from the pectoralis profundus muscle of running dogs (Carrier et al., 2006) and a variety of primates during walking (Larson and Stern, 2007), which suggest that the retractor muscles do not contribute to retraction of the forelimb during the support phase.

In this investigation, we studied the locomotor function of the primary protractor and retractor muscles of the forelimb of domestic dogs during trotting. Our objectives were to determine whether or not the forelimb functions as a strut during constant-speed running and to characterize the locomotor function of these muscles in a mammalian cursor. We define locomotor function as the role the muscle plays in, or what the muscle contributes to, a running step. To test hypotheses of function, we monitored changes in the recruitment (i.e. electromyography) of these muscles in response to controlled manipulations of locomotor forces and moments. Specifically, we added mass to the trunk to increase the inertia and weight of the body; we added mass to the distal forelimbs to increase the inertia of the limbs; we ran the dogs up- and downhill to increase the fore/aft forces that the limbs must apply to the substrate; and we pulled horizontally on the trunk (i.e. forward, backward, ipsilaterally and contralaterally to forelimb support) to increase the horizontal forces applied to the substrate. The rationale of this approach is that changes in forelimb mechanical requirements must be met by correlated changes in the recruitment of the muscles that transmit forces and moments between the forelimb and trunk. Hence, we interpret changes in recruitment of a muscle associated with the manipulations of locomotor forces and moments to reflect a functional role for that muscle. The limitation of this approach is that electromyography does not provide information on muscle force production, length change or work production. Nevertheless, the recruitment response of a muscle to force manipulations does allow functional analysis in muscles for which *in vivo* force cannot be recorded, such as the muscles studied here, and also allows analysis of the integrated action of a large number of muscles.

In the case of the hypothesis that the forelimb behaves as a strut during running at constant speed on level surfaces, the prediction is that the protractor and retractor muscles of the limb will function to produce the swing phase of the limb but will not participate in the production of motion of the limb during stance phase, the period when the limb functions as a strut. Thus, we expect that recruitment of these extrinsic appendicular muscles will increase when mass is added to the limb, to increase the work of swing phase, but that there will not be an increase in recruitment when mass is added to the trunk, to increase the work done in braking and propulsion of the body. Additionally, when dogs run uphill or pull forward against a rearward-directed force, we expect the timing of activity of the forelimb retractor muscles to change to coincide with stance phase because under these circumstances the limb must function as a lever and active retraction of the limb is required for propulsion.

An aspect of exercise physiology for which the strut hypothesis has implications is the integration of lung ventilation and locomotion. Sustained vigorous locomotion characterizes mammals and is made possible, in part, by an ability to breathe during running (Bramble and Carrier, 1983; Carrier, 1987). For the forelimb to function as a strut, the moments at its fulcrum on the trunk must be minimized. If moments at the shoulder are minimized, locomotor forces imposed on the trunk by the extrinsic forelimb muscles will also be minimized, reducing potential conflicts between the locomotor and ventilatory functions of individual axial muscles. Thus, an additional goal of this investigation was to determine whether or not the activity patterns of the forelimb protractors and retractor muscles are consistent with observed patterns of airflow in trotting dogs.

MATERIALS AND METHODS

Activity of six 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 m s^{-1}) on a motorized treadmill. Mean body mass of the six dogs was 24±4.2 kg (s.d.). Each dog was obtained from a local animal shelter and trained to run on a treadmill. The muscles studied were the m. pectoralis superficialis descendens, the posterior portion of the m. pectoralis profundus, the ventral and dorsal portions of the m. latissimus dorsi, the m. omotransversarius, the m. cleidobrachialis, and the cervical and thoracic parts of the m. trapezius. The anatomy of these muscles is described in Evans (Evans, 1993) and illustrated in Fig. 1. Recording of muscle activity began on the fourth day after surgery and continued for 5–6 days. The electrodes were removed 10–11 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. Surgical implantation of electrodes and recording were described in detail previously (Carrier et al., 2006).

Locomotor force manipulations

To improve our understanding of the locomotor function of the six muscles, we monitored changes in EMG pattern in response to manipulations of the locomotor forces. To increase the vertical forces on the forelimbs due to gravity, the dogs ran with a backpack containing masses of 0% (control), 8% or 12% of body mass. These are added masses that previous studies in our lab (Fife et al., 2001; Carrier et al., 2006) have shown to have minimal effects on the kinematics of running but that elicit significant EMG responses from locomotor muscles. The 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).

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 downhill at slopes of 0° (control), 10° and 14° from the horizontal. When the dogs ran uphill, the incline increased the positive (propulsive) work that the

dog had to do in the fore/aft direction. Conversely, when the dogs ran downhill, they did more negative (braking) work in the fore/aft direction. Ten and 14° are inclines that dogs can traverse using a trotting gait but require significant increases in the activity of muscles associated with protraction and retraction of the limbs (Carrier et al., 2006). 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.

We also manipulated the fore/aft and lateral forces by applying horizontally oriented forces directed forward, rearward, ipsilateral and contralateral 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 in the most appropriate manner for each of the pulling directions. The applied force was monitored with a force transducer that was in-series with the leash. For the forward-directed pulls, the force was applied *via* a muzzle over the dog's snout. Rearward-directed forces were applied with a sled racing harness. The ipsilateral and contralateral forces were applied with

a loop around the neck and another loop around the dog's trunk at the abdomen. The muzzle was a greyhound racing muzzle 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. This method applied the forward-directed force roughly inline with the body axis. Similarly, the loops around the neck and abdomen allowed the application of a well-balanced laterally directed force. To determine if a correlation existed between the level of horizontal force applied and the recruitment of the muscle, a wide range of horizontal forces was applied to each dog. 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 during a given trial.

To increase the forces required to protract and retract the forelimbs during the swing phase of a running step, we added mass of 0% (control), 1% or 2% of body mass to the dog's wrists. These added masses are small enough that stride kinematics are not altered dramatically but result in significant increases in the activity of muscles associated with the production of swing phase (Carrier et al., 2006).

Each of these force manipulations was run on separate days to minimize fatigue. Separate control trials were run for each force manipulation. Control trials consisted of the dogs trotting unencumbered on a level treadmill at the same speed as that of the force manipulation trials. In many cases, control trials were run both before and after the force manipulations to provide an indication of the influence of fatigue on the EMGs. Because each set of force manipulations has a separate set of control trials, there is some variation in the control traces for several of the muscles. We attribute this variation to changes in the performance of the individual electrodes from day to day and to the fact that in some cases an electrode ceased working, forcing us to use the second electrode in a muscle for some of the manipulation experiments.

Fig. 1. Illustrations of the extrinsic appendicular muscles of the canid pectoral girdle, showing the location of the electrode placements used in this study. (A) Lateral view of the m. trapezius pars thoracica (1), m. trapezius pars cervicalis (2), m. omotransversarius (3), m. cleidobrachialis (4), m. pectoralis profundus (5) and m. latissimus dorsi (6, 7). (B) Ventral view of the m. cleidobrachialis (4), m. pectoralis profundus (5) and m. pectoralis superficialis descendens (8).

Analysis of EMG 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 forelimb 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.
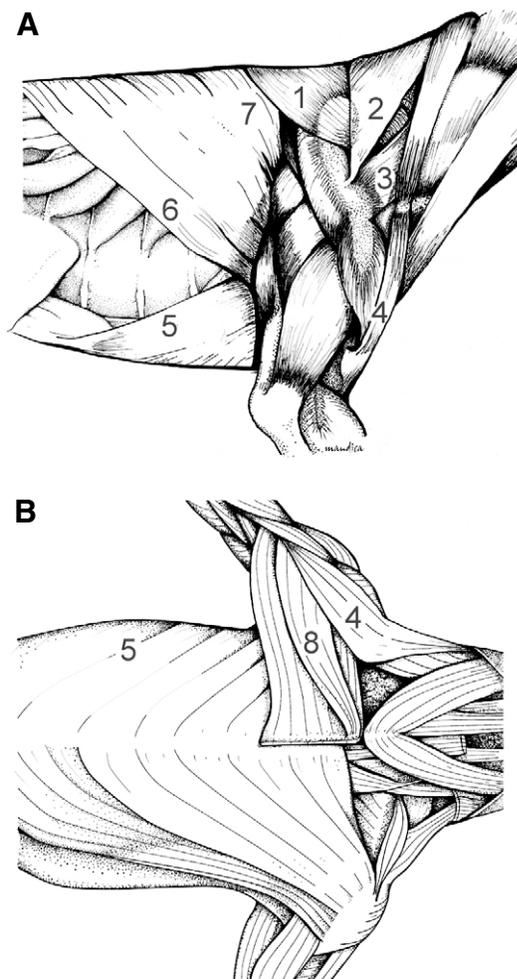
Data were collected for the different force manipulations on separate days, necessitating a minimum of four recording days (i.e. added trunk mass, hills, added wrist mass, added horizontal force) for each subject. Separate control trials were collected each day and for each force manipulation. During the control trials, the dogs trotted unimpeded (i.e. with no force manipulation) 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).

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. We interpreted an increase in integrated area of the EMG as an increase in the number of motor units recruited, an increase in the duration of recruitment or an increase in both. If there was no effect of the manipulation, the result would be 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 means ± 1 s.e.m.

To test if application of horizontally directed forces changed the recruitment of a given muscle, we used regression of scaled force and EMG area. Thirty-five to 40 strides were sampled for each force manipulation (e.g. lateral pull to the ipsilateral side in dog #1). The rectified integrated area of each EMG sample was determined by summing the data points for each stride. The mean force applied to the dog during each of the sampled strides was determined from the force transducer in series with the leash. Each set of 35–40 samples from each dog was normalized such that values of integrated EMG area and applied force ranged from zero to one. This was accomplished by subtracting the minimum value in the set from every value and then dividing each value by the range of values. Thus, the data from each dog were adjusted to the same scale. We then tested for a significant regression at $P<0.05$ of the normalized EMG area against normalized force with all dogs included in a single regression.

In general, the force manipulations resulted in small or no changes in the periods of ipsilateral forelimb support and swing phases (Carrier et al., 2006). In the steep downhill trials (14.5°), 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 was increased significantly. The swing phase of the 2% wrist mass trials was most dramatically affected, 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.

RESULTS
M. pectoralis superficialis descendens

When trotting at constant speed, the descending portion of the superficial pectoralis muscle was active during the latter half of the support phase of the ipsilateral limb (Figs 2–5). Activity began at roughly 50% of the support phase, increased to peak activity at 75% of support, declined rapidly and continued at a low level into the beginning of ipsilateral swing phase, ending at approximately 25% of swing phase.

Adding mass to the trunk tended to increase the integrated activity of this muscle (10–40%), but the effect was not significant in any of the eight trunk-loading manipulations (Table 1). Furthermore, when mass was added to the trunk, the period of the activity of the muscle did not change relative to the unloaded control trials (Fig. 2).

Trotting both uphill and downhill increased the activity of this muscle (Figs 3 and 4). When the dogs ran uphill, the mean activity increased by 50 and 90% (Table 1) during the period when the muscle was active in the control trials (Fig. 3). When the subjects trotted downhill, mean activity of the descending pectoralis muscle increased by 2–2.5-fold above that observed during level trotting (Table 1) and the period of activity increased to be associated with most of the support phase of the ipsilateral limb (Fig. 4).

Addition of mass to the wrists was associated with a substantial increase in mean activity of the descending portion of the pectoralis muscle, but the increase was significant in only the trials with 2% of body mass added (Table 1). The period of activity during these added mass trials included the period at the end of support, as observed during the control trials, and continued into the first third of ipsilateral swing phase (Fig. 5).

All four manipulations of horizontal force showed significantly positive slopes of normalized EMG area regressed against normalized applied force (Table 2).

Table 1. Mean response relative to control, standard error of change, and significance of change from control of the *M. pectoralis superficialis descendens* to the different force manipulations

Manipulation	N	Mean change	Standard error	P-value
Anterior-trunk mass				
8%	6	1.378	0.268	0.1087
12%	6	1.301	0.157	0.0561
Mid-trunk mass				
8%	6	1.306	0.197	0.0905
12%	6	1.175	0.138	0.1307
Posterior-trunk mass				
8%	6	1.204	0.176	0.1492
12%	6	1.153	0.11	0.1116
Ant./post. mass				
8%	6	1.106	0.108	0.1857
12%	6	1.413	0.235	0.0697
Hills				
Uphill 10°	6	1.539	0.154	0.0087*
Uphill 14°	6	1.886	0.245	0.0076*
Downhill 10°	6	2.018	0.338	0.0149*
Downhill 14°	6	2.539	0.532	0.0171*
Wrist mass				
1%	6	2.122	0.709	0.0871
2%	6	2.778	0.872	0.0486*

*Significant at $P<0.05$.

M. pectoralis profundus (posterior portion)

When the dogs trotted at constant speed, the posterior portion of the deep pectoralis was active during the latter half of the swing phase of the ipsilateral limb (Figs 2–5). It became active midway through the swing phase, reached peak activity at 70% of ispsilateral swing phase, and activity diminished rapidly such that the muscle was silent during the last 10% of swing phase. During trotting at constant speed, the muscle was not active during the support phase of the ipsilateral limb.

The addition of mass to the trunk had little effect on the activity of the posterior portion of the deep pectoralis muscle (Table 3, Fig. 2). Activity of the muscle did not increase significantly in any of eight trunk-loading manipulations.

Running uphill and downhill induced dramatic changes in both the amplitude and period of activity of the posterior portion of the deep pectoralis muscle (Table 3, Figs 3 and 4). Trotting uphill did not change the timing of initiation of activity of the muscle, but the period of activity lengthened such that the muscle remained active throughout the first half of ipsilateral support phase (Fig. 3). The mean level of activity increased 2.8-fold during trotting uphill at an angle of 10° and 3.8-fold when trotting uphill at 14° (Table 3). By

contrast, trotting downhill had little effect on the period of activity during ipsilateral swing phase (Fig. 4) but resulted in a 50% reduction in the mean amplitude of activity (Table 3).

Addition of mass to the wrists increased the amplitude of activity, but the increase was significant for only the 1% trials (Table 3). The period of activity in these trials remained confined to ipsilateral swing phase, beginning somewhat earlier in swing phase (Fig. 5).

Of the four horizontal force manipulations, the rearward-directed forces resulted in increased activity whereas the forward-directed forces resulted in significant decreases in activity from the posterior deep pectoralis (Table 2). Activity of this muscle was positively correlated with the contralateral-directed forces but was not correlated with the ipsilateral-directed forces.

M. latissimus dorsi

During the control trials, in which the dogs trotted at constant speed, activity at both recording sites in the latissimus dorsi muscle was similar in timing to that observed in the posterior portion of the deep pectoralis muscle (Figs 2–5). At both sites, activity of the latissimus dorsi began midway through the swing phase of the
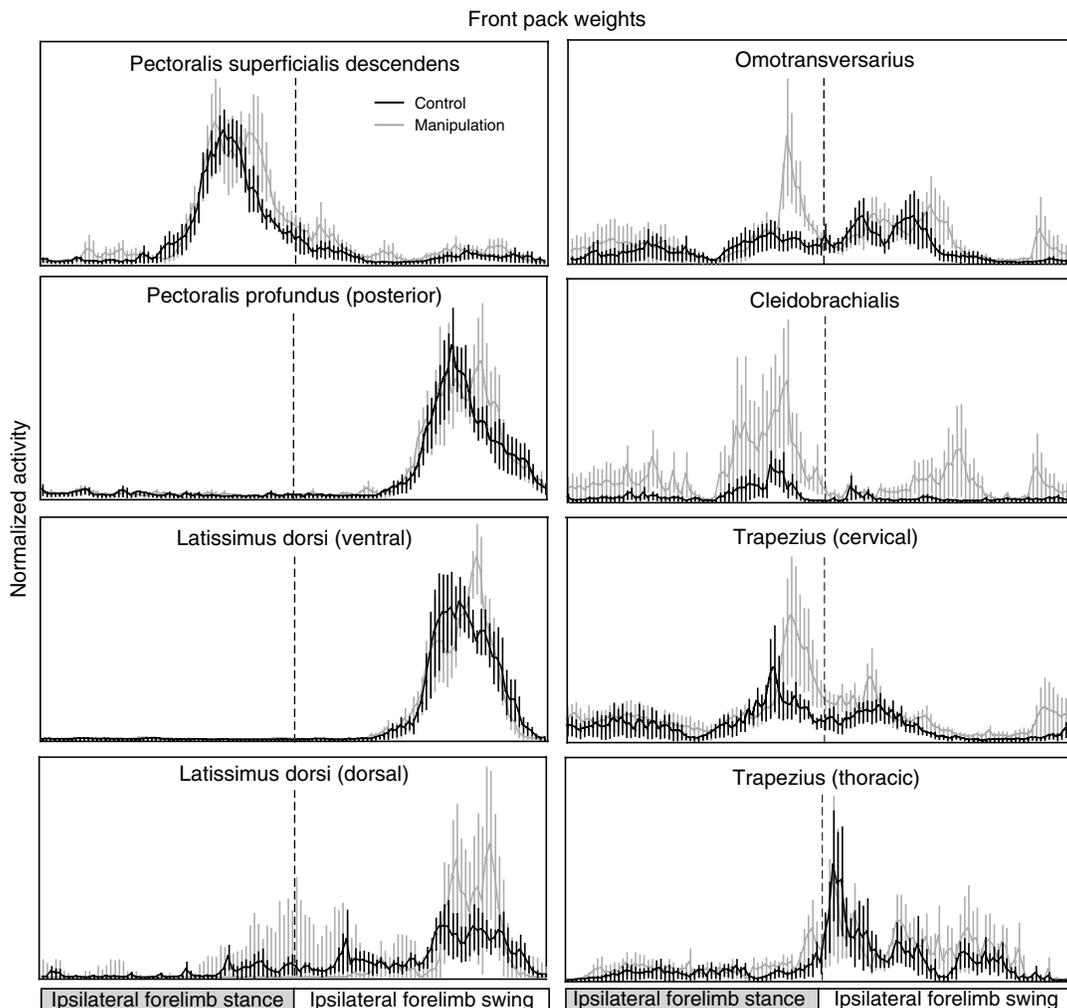

Fig. 2. Mean normalized electromyograms (EMGs) from six dogs when they trotted with 12% of body mass carried in a backpack located over their pectoral girdle (i.e. anterior-trunk loading manipulation). For each muscle, the black line represents the average EMG when the dogs trotted on the level without added mass (control) and the gray 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 standard error of the mean for each sampling bin.
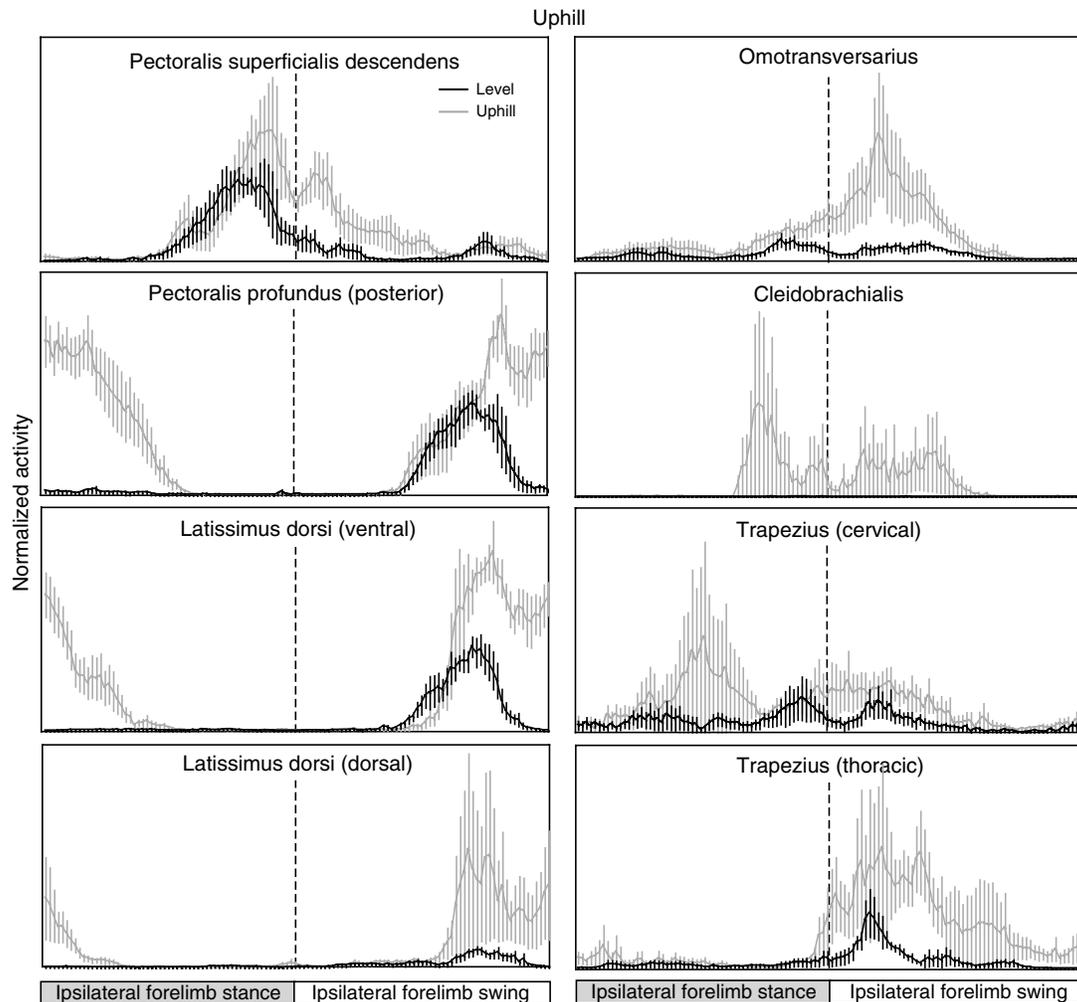
Uphill

Fig. 3. Mean normalized EMGs from six dogs when they trotted uphill 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 gray 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 standard error of the mean for each sampling bin.

ipsilateral forelimb, reached peak activity at approximately 70% of swing phase, and then activity ceased shortly before the beginning of the support phase. Thus, when the dogs trotted at constant speed, activity of the latissimus dorsi muscle was confined to the second half of ipsilateral swing phase.

Adding mass to the trunk tended to increase the activity of the ventral portion of the latissimus dorsi, but the increased activity was not always significantly different from that of the unweighted trials (Table 4). When the result was significantly different, the increase ranged from 11 to 21%. The increased activity occurred during the same period as that of the control trials (Fig. 2). Although activity tended to increase in the dorsal portion of the latissimus dorsi when the trunk was loaded with additional mass, the increase was not significantly different from the control trials (Table 5).

Activity of the latissimus dorsi muscle increased when the dogs trotted uphill and decreased when they ran downhill (Figs 3 and 4). The changes relative to the control trials were substantial, 2–6-fold increases when the dogs ran uphill and 40–60% decreases when the dogs ran downhill (Tables 4 and 5). When running uphill, the period of activity also increased, such that activity of the muscle extended into the first third of ipsilateral support phase (Fig. 3).

Timing of the activity, however, did not change relative to control trials when the dogs trotted downhill (Fig. 4).

Adding mass to the wrists increased the activity of latissimus dorsi muscle (Fig. 5). However, the increased activity was significantly different from the controls only in the recordings from the ventral portion of the muscle (Tables 4 and 5). In the ventral portion of the muscle, timing of the activity did not change when mass was added to the wrists.

The response of both dorsal and ventral recording sites of the latissimus dorsi muscle to the horizontal force manipulations was similar. Both sites exhibited significant positive correlations between muscle activity and rearward-directed forces and significant negative correlations with forward-directed forces (Table 2). At both sites, muscle activity was positively correlated with contralateral-directed forces but not with ipsilateral-directed forces.

M. omotransversarius

When the dogs trotted at constant speed, activity of the omotransversarius muscle tended to be tri-phasic (Figs 2–5). A low level of activity was observed during the first half of ipsilateral limb support. Somewhat higher activity occurred during the last third of
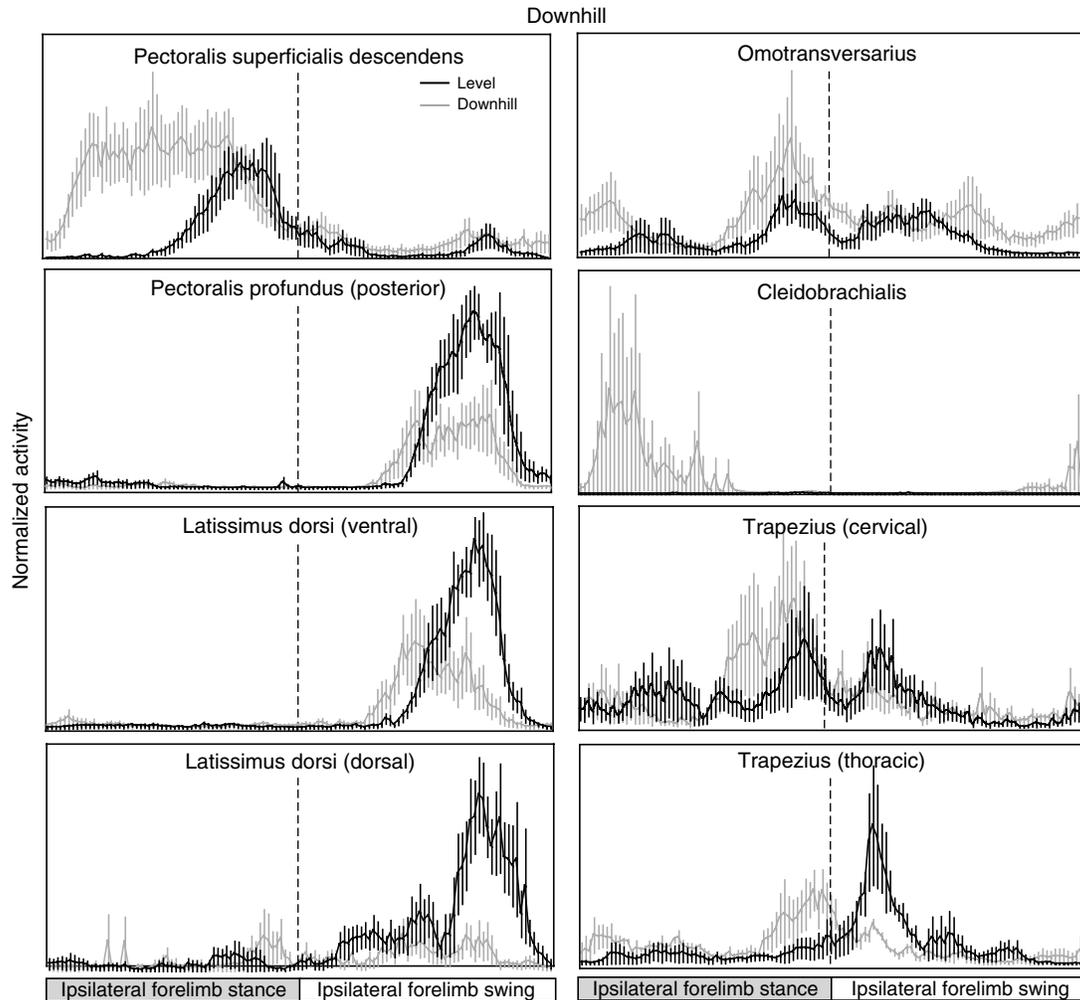
Fig. 4. Mean normalized EMGs from six dogs when they trotted downhill on an incline of 14° to the horizontal (i.e. fore/aft force manipulation). For each muscle, the black line represents the average EMG when the dogs trotted on the level (control) and the gray line represents the average EMG when the 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 standard error of the mean for each sampling bin.

ipsilateral support, and a third phase of activity occurred during the first half of ipsilateral swing phase.

Adding mass to the trunk tended to produce small increases in activity of the omotransversarius muscle (Table 6). Only three of the eight added mass manipulations, however, resulted in statistically significant differences. In these trials, the increased activity occurred during the last 20% of ipsilateral support phase (Fig. 2).

Activity of the omotransversarius muscle increased when the dogs ran both up- and downhill. Running uphill produced a 3–4-fold increase in activity relative to running on the level treadmill (Table 6). The increased activity during uphill running occurred during the first half of ipsilateral swing phase (Fig. 3). The increased activity during trotting downhill was significant at the steeper 14° slope but not at the 10° slope (Table 6). The increase in activity during downhill running was most pronounced at the end of ipsilateral swing and the beginning of ipsilateral support phase (Fig. 4).

The addition of mass to the wrists produced increases of activity of 2–3.5-fold above that of the control trials (Table 6). The increased activity was associated with the end of ipsilateral support phase and the first half of ipsilateral swing phase (Fig. 5).

Activity of the omotransversarius muscle was positively correlated with applied force in all four of the horizontal force manipulations (Table 2).

M. cleidobrachialis

During constant-speed trotting, the cleidobrachialis exhibited a very low level of activity. In a number of our control recordings, no muscle activity was discernible. Nevertheless, low-level activity was present during the last 20% of ipsilateral support phase (in four of the five dogs for which we have recordings) and the first 20% of ipsilateral swing phase (in two of the five dogs for which we have recordings) (Fig. 2). This activity, however, was generally of very low amplitude relative to the activity recorded during several of the force manipulations (discussed below).

Adding mass to the trunk tended to increase the activity of the cleidobrachialis (Table 7). However, only three of the eight added trunk-mass manipulations resulted in significant increases in activity over that of the control trials. The greatest increase in activity occurred during the last portion of ipsilateral support (Fig. 2) and was most pronounced when the mass was added to the anterior trunk.
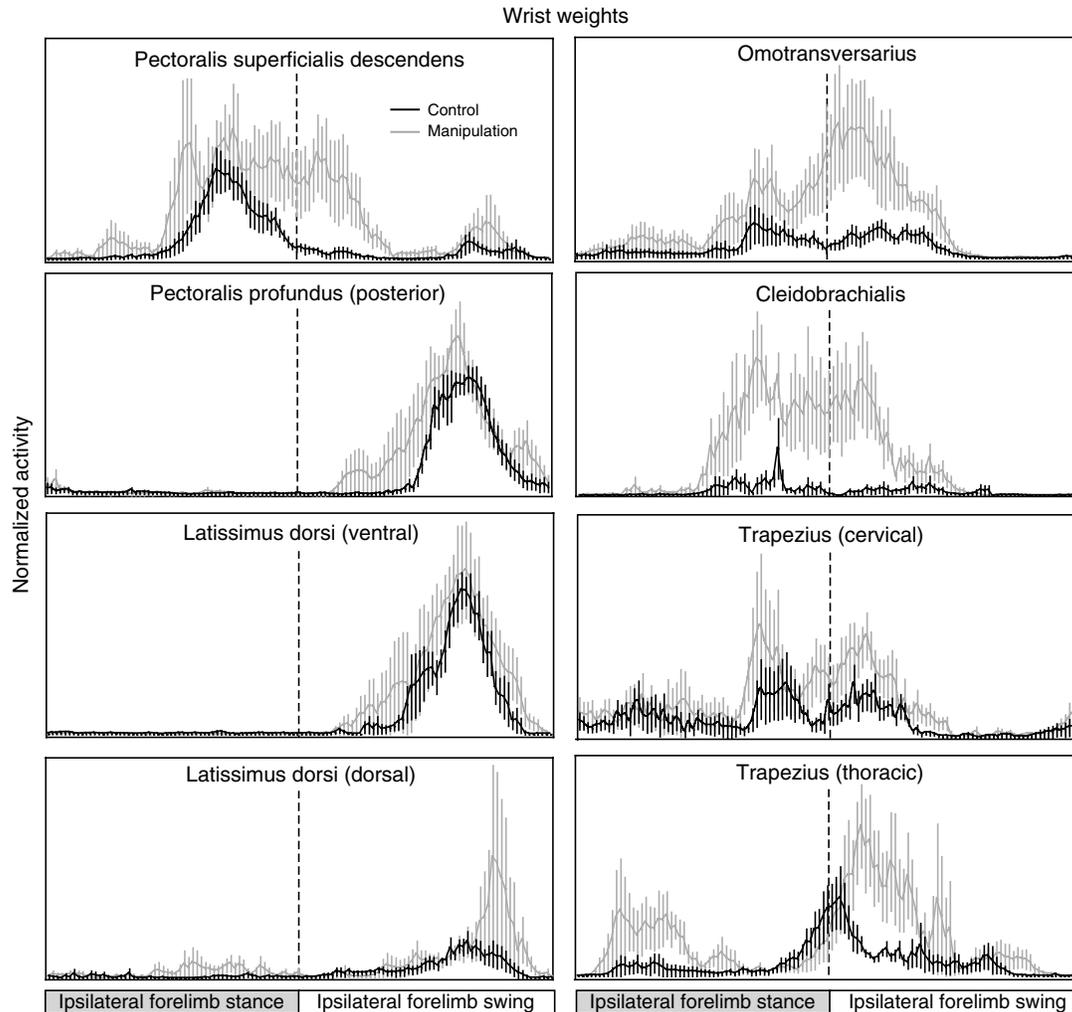
Wrist weights

Fig. 5. Mean normalized EMGs from six dogs when they trotted 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 gray 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 standard error of the mean for each sampling bin.

Activity of the cleidobrachialis muscle increased dramatically when the dogs trotted uphill and downhill (Figs 3 and 4). The increases in integrated activity were substantial, between 35 and 325-fold when the dogs ran uphill and between 21 and 147-fold when the dogs ran downhill (Table 7). Although the observed responses were qualitatively the same in each of the five dogs for which we have data, variation in the magnitude of the change of muscle activity made the results for the uphill and downhill manipulations non-significant. The high variation occurred because the muscle exhibited almost no activity during control trials in several of the dogs. Because the data were normalized with the average activity level of the control trials, we divided the recordings from several of the dogs by very small normalization values. Normalizing the data with a value close to zero for some of the subjects, but not others, produced high variation in the magnitude of the change in muscle activity associated with hill running. Importantly, the increased activity during uphill running occurred during the same period as observed in the control trials, the end of support and first half of swing phase (Fig. 3). By contrast, during downhill running the period of muscle activity switched to the first half of ipsilateral support phase (Fig. 4).

The addition of mass to the wrists produced increases of activity of 3 to ~13-fold above that of the control trials (Table 7). The increased activity was associated with the end of ipsilateral support phase and the first half of ipsilateral swing phase (Fig. 5).

Activity of the cleidobrachialis muscle was positively correlated with applied force for all four of the horizontal force manipulations (Table 2).

Cervical portion of the m. trapezius

During constant speed trotting, the cervical portion of the trapezius muscle exhibited a pattern of tri-phasic activity that was similar to the pattern observed in the omotransversarius muscle (Figs 2–5). A low level of activity was observed during the first half of ipsilateral limb support. Somewhat higher activity occurred during the last third of ipsilateral support. A third phase of activity occurred during the first half of ipsilateral swing phase.

Adding mass to the trunk tended to produce small increases in activity of the cervical portion of the trapezius muscle, but none of the eight manipulations exhibited a significant increase (Table 8). The increase in activity occurred during the last 20% of ipsilateral support and first 20% of ipsilateral swing phase (Fig. 2).

Table 2. Relationship between applied horizontal force and EMG area for eight recording sites in six extrinsic forelimb muscles

Muscle manipulation	Slope	r^2	P-value
Pectoralis super. descending			
Rear pull	0.26	0.08	<0.0001*
Front pull	0.44	0.22	<0.0001*
Ipsilateral pull	0.47	0.27	<0.0001*
Contralateral pull	0.33	0.18	<0.0001*
Pectoralis profundus (post.)			
Rear pull	0.42	0.20	<0.0001*
Front pull	−0.17	0.04	0.0086*
Ipsilateral pull	0.01	0.0002	0.8457
Contralateral pull	0.15	0.04	0.0069*
Latissimus dorsi (ventral)			
Rear pull	0.72	0.64	<0.0001*
Front pull	−0.39	0.18	<0.0001*
Ipsilateral pull	0.14	0.02	0.0778
Contralateral pull	0.22	0.09	<0.0001*
Latissimus dorsi (dorsal)			
Rear pull	0.73	0.63	<0.0001*
Front pull	−0.50	0.32	<0.0001*
Ipsilateral pull	0.13	0.02	0.0815
Contralateral pull	0.16	0.05	0.0089*
Omotransversarius			
Rear pull	0.42	0.26	<0.0001*
Front pull	0.47	0.21	<0.0001*
Ipsilateral pull	0.15	0.04	0.0086*
Contralateral pull	0.34	0.23	<0.0001*
Cleidobrachialis			
Rear pull	0.43	0.27	<0.0001*
Front pull	0.47	0.26	<0.0001*
Ipsilateral pull	0.35	0.21	<0.0001*
Contralateral pull	0.34	0.19	<0.0001*
Cervical trapezius			
Rear pull	0.14	0.03	0.0154*
Front pull	0.20	0.05	0.0014*
Ipsilateral pull	0.10	0.01	0.1417
Contralateral pull	0.12	0.02	0.0543
Thoracic trapezius			
Rear pull	0.29	0.13	<0.0001*
Front pull	0.50	0.33	<0.0001*
Ipsilateral pull	0.17	0.05	0.0058*
Contralateral pull	0.49	0.43	<0.0001*

*Significant at P<0.05.

Table 3. Mean response relative to control, standard error of change, and significance of change from control of the *M. pectoralis profundus* (posterior portion) to the different force manipulations

Manipulation	N	Mean change	Standard error	P-value
Anterior-trunk mass				
8%	6	1.382	0.189	0.0567
12%	6	1.218	0.234	0.2018
Mid-trunk mass				
8%	6	1.229	0.139	0.0806
12%	6	1.3	0.223	0.1179
Posterior-trunk mass				
8%	6	0.89	0.036	0.9854
12%	6	1.103	0.089	0.1486
Ant./post. mass				
8%	6	0.967	0.053	0.72
12%	6	0.984	0.078	0.5766
Hills				
Uphill 10°	6	2.79	0.181	<0.0001*
Uphill 14°	6	3.774	0.33	0.0002*
Downhill 10°	6	−0.537	0.113	0.0047*
Downhill 14°	6	−0.503	0.135	0.0071*
Wrist mass				
1%	6	1.321	0.125	0.0250*
2%	6	2.239	0.673	0.0625

*Significant at P<0.05.

Table 4. Mean response relative to control, standard error of change, and significance of change from control of the *M. latissimus dorsi* (ventral portion) to the different force manipulations

Manipulation	N	Mean change	Standard error	P-value
Anterior-trunk mass				
8%	6	1.194	0.066	0.0159*
12%	6	1.043	0.086	0.3207
Mid-trunk mass				
8%	6	1.104	0.054	0.0578
12%	6	1.211	0.086	0.0289*
Posterior-trunk mass				
8%	6	1.091	0.081	0.1552
12%	6	1.117	0.039	0.0144*
Ant./post. mass				
8%	6	1.11	0.031	0.008*
12%	6	1.101	0.069	0.1032
Hills				
Uphill 10°	6	2.089	0.191	0.0012*
Uphill 14°	6	3.47	0.463	0.0016*
Downhill 10°	6	−0.568	0.139	0.0122*
Downhill 14°	6	−0.633	0.158	0.0340*
Wrist mass				
1%	6	1.294	0.071	0.0046*
2%	6	1.491	0.165	0.0156*

*Significant at P<0.05.

Running uphill resulted in increased activity in the cervical portion of the trapezius muscle (Table 8). The timing of the activity changed such that the greatest activity occurred during the middle of ipsilateral stance and first half of swing phase (Fig. 3). Activity of this muscle did not change significantly during trotting downhill (Table 8, Fig. 4).

The most significant response we observed in the cervical portion of the trapezius muscle occurred in the trials in which mass was added to the wrists. This manipulation produced an approximately 2-fold increase in activity with the addition of both 1% and 2% of body mass added to the wrists (Table 8). The increased activity occurred during the last third of ipsilateral support phase and first third of ipsilateral swing phase (Fig. 5).

Only the forward- and rearward-directed pulls produced a significant correlation between muscle activity and applied force in the cervical portion of the trapezius muscle (Table 2).

Thoracic portion of the m. trapezius

The primary activity of the thoracic portion of the trapezius muscle in trotting dogs occurs during the first third of ipsilateral swing phase (Figs 2–5). In several of the dogs, low levels of activity continued through the first half to two-thirds of the swing phase.

Table 5. Mean response relative to control, standard error of change, and significance of change from control of the *M. latissimus dorsi* (dorsal portion) to the different force manipulations

Manipulation	N	Mean change	Standard error	P-value
Anterior-trunk mass				
8%	4	1.541	0.334	0.1017
12%	4	2.171	0.754	0.109
Mid-trunk mass				
8%	4	1.318	0.475	0.2758
12%	4	1.59	0.682	0.2253
Posterior-trunk mass				
8%	4	1.032	0.089	0.3717
12%	4	0.849	0.108	0.8714
Ant./post. mass				
8%	4	0.796	0.117	0.9098
12%	4	2.928	2.003	0.2034
Hills				
Uphill 10°	5	3.4	1.472	0.0892
Uphill 14°	5	6.354	3.5	0.1004
Downhill 10°	5	−0.363	0.039	<0.0001*
Downhill 14°	5	−0.399	0.09	0.0013*
Wrist mass				
1%	5	1.636	0.408	0.0969
2%	5	2.25	0.71	0.0764

*Significant at *P*<0.05.

Table 7. Mean response relative to control, standard error of change, and significance of change from control of the *M. cleidobrachialis* to the different force manipulations

Manipulation	N	Mean change	Standard error	P-value
Anterior-trunk mass				
8%	5	3.219	0.735	0.0196*
12%	5	16.107	12.504	0.1468
Mid-trunk mass				
8%	5	1.688	0.365	0.0663
12%	5	5.437	2.674	0.0862
Posterior-trunk mass				
8%	5	2.404	0.169	0.0006*
12%	5	6.093	3.701	0.1204
Ant./post. mass				
8%	5	2.978	1.234	0.0921
12%	5	4.883	1.458	0.0281*
Hills				
Uphill 10°	5	35.224	20.397	0.0843
Uphill 14°	5	325.564	300.881	0.1707
Downhill 10°	5	21.014	13.238	0.1026
Downhill 14°	5	147.442	128.609	0.1592
Wrist mass				
1%	5	3.396	1.086	0.0392*
2%	5	12.818	4.73	0.0273*

*Significant at *P*<0.05.

Adding mass to the trunk did not produce significant changes in the level of activity recorded from the thoracic trapezius muscle (Table 9, Fig. 2).

Running uphill resulted in a 2–4-fold increase in activity of the thoracic trapezius muscle (Table 9). Surprisingly, the increase occurred not during support phase but during the first half of ipsilateral swing phase (Fig. 3). Running downhill did not produce a significant change in the integrated activity of the thoracic trapezius muscle (Table 9), but there did appear to be a phase shift in the timing of the activity such that the peak activity occurred at the end of ipsilateral support rather than the beginning of ipsilateral swing phase (Fig. 4).

Table 6. Mean response relative to control, standard error of change, and significance of change from control of the *M. omotransversarius* to the different force manipulations

Manipulation	N	Mean change	Standard error	P-value
Anterior-trunk mass				
8%	6	1.306	0.134	0.0353*
12%	6	1.551	0.346	0.0864
Mid-trunk mass				
8%	6	1.274	0.121	0.0363*
12%	6	1.439	0.238	0.0622
Posterior-trunk mass				
8%	6	1.135	0.112	0.1406
12%	6	1.224	0.081	0.0198*
Ant./post. mass				
8%	6	1.169	0.255	0.2689
12%	6	1.276	0.184	0.0971
Hills				
Uphill 10°	6	3.066	1.244	0.0215*
Uphill 14°	6	3.932	0.448	0.0325*
Downhill 10°	6	1.225	0.767	0.0961
Downhill 14°	6	2.004	0.15	0.0375*
Wrist mass				
1%	6	2.174	0.659	0.0676
2%	6	3.517	0.921	0.0206*

*Significant at *P*<0.05.

Table 8. Mean response relative to control, standard error of change, and significance of change from control of the cervical portion of the *M. trapezius* to the different force manipulations

Manipulation	N	Mean change	Standard error	P-value
Anterior-trunk mass				
8%	6	1.093	0.085	0.1627
12%	6	1.629	0.511	0.1365
Mid-trunk mass				
8%	6	1.019	0.079	0.4083
12%	6	1.375	0.213	0.0695
Posterior-trunk mass				
8%	6	0.989	0.07	0.559
12%	6	1.485	0.26	0.0604
Ant./post. mass				
8%	6	1.088	0.208	0.3454
12%	6	1.292	0.373	0.2348
Hills				
Uphill 10°	6	1.878	0.408	0.0421*
Uphill 14°	6	2.516	0.824	0.0625
Downhill 10°	6	0.895	0.122	0.7863
Downhill 14°	6	1.195	0.28	0.2583
Wrist mass				
1%	6	1.956	0.256	0.0068*
2%	6	1.899	0.228	0.0055*

*Significant at *P*<0.05.

Table 9. Mean response relative to control, standard error of change, and significance of change from control of the thoracic portion of the *M. trapezius* to the different force manipulations

Manipulation	N	Mean change	Standard error	P-value
Anterior-trunk mass				
8%	6	1.48	0.718	0.267
12%	6	1.36	0.445	0.2276
Mid-trunk mass				
8%	6	1.084	0.163	0.3149
12%	6	1.575	0.491	0.1469
Posterior-trunk mass				
8%	6	1.106	0.156	0.2643
12%	6	1.605	0.397	0.0941
Ant./post. mass				
8%	6	1.405	0.348	0.1483
12%	6	1.267	0.222	0.1415
Hills				
Uphill 10°	5	2.289	1.421	0.0337*
Uphill 14°	5	4.221	0.126	0.043*
Downhill 10°	5	0.864	0.517	0.7721
Downhill 14°	5	1.043	0.165	0.3749
Wrist mass				
1%	5	1.627	0.392	0.0925
2%	5	2.495	0.703	0.0504*

Addition of mass to the wrists tended to produce an increase in activity of the thoracic trapezius muscle, but the increase was only significant for the 2% body mass addition (Table 9). The increase in activity occurred during the first half of ipsilateral swing phase and there was a smaller pulse of activity during the first half of ipsilateral support phase (Fig. 5).

Activity of the thoracic portion of the trapezius muscle was positively correlated with applied force in all four of the horizontal force manipulations (Table 2).

DISCUSSION
Limitations of the approach

The approach used in this study of monitoring changes in EMG in response to force manipulations to investigate muscle function is limited because the recordings do not provide information on muscle force production or changes in length, both of which are essential to an unambiguous understanding of the function of individual muscles *in vivo*. Nevertheless, we chose the approach for several reasons. First, measurement of *in vivo* force production from a muscle typically requires instrumentation of a distinct in-series tendon, such as the tendons commonly associated with the distal muscles of the limb, with tendon buckle cuffs (Biewener et al., 1998b; Biewener and Corning, 2001; Daley and Biewener, 2003) or strain gages (Roberts et al., 1997). None of the muscles analyzed in this study have pronounced in-series tendons, making this approach impossible. The monitoring of muscle force *via* measurements of bone strain, as has been accomplished in the avian pectoralis muscle (Biewener et al., 1998a), was also deemed to be impractical in this case because of the relatively large size and complexity of the muscle attachments to the scapula and humerus. Also, we were unwilling to sacrifice the subjects used in this study after the recordings to allow calibration of the strain gages. Finally, the method of recording changes in recruitment associated with specific force manipulations allows the testing of specific hypotheses of muscle function in a large number of muscles simultaneously.

Descending portion of the pectoralis superficialis muscle

The descending portion of the superficial pectoralis 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 forelimb protraction. When the dogs trotted at constant speed on a level treadmill, this muscle was active during the last half of the support phase, which is appropriate to protract the limb at the beginning of swing phase. The increase in recruitment during this period when mass was added to the wrists supports this interpretation. A similar increase during the end of support and the beginning of swing phase when running uphill also suggests that the descending portion of the pectoralis contributes to protraction of the limb in swing phase because the limb must be lifted upwards when running uphill. The greatly increased activity early in the support phase when the dogs ran downhill and when the dogs were pulled forward by the experimenter suggests that this muscle provides a protraction moment at the shoulder when dogs decelerate in the forward direction.

Adding mass to the anterior trunk resulted in slight, but not significant, increases in activity at the very end of the support phase. Previous analysis (Carrier et al., 2006) found adding mass to the anterior trunk resulted in a small (3%) reduction in the duration of swing phase. Thus, the small elevation of activity of the descending portion of the pectoralis muscle may be associated with the need to protract the limb more rapidly in swing phase. Pulling laterally increased the activity of the muscle, suggesting a role in mediolateral stabilization of the body.

In summary, the descending portion of the superficial pectoralis muscle functions to initiate the swing phase of the step cycle by protracting the limb and is active during deceleration in the forward direction. During constant-speed trotting on a level treadmill, the muscle is not active during the normal braking portion (i.e. first half) of the support phase of the step. These results are consistent with those previously reported for a dog by Tokuriki (Tokuriki, 1973).

Pectoralis profundus and latissimus dorsi muscles

The pectoralis profundus and latissimus dorsi muscles exhibited a pattern of activity during level trotting and responded to the force manipulations in ways that are consistent with the function of forelimb retraction. During constant-speed running on a level treadmill, both muscles were active during the last half of the swing phase, consistent with braking and reversing the forward motion of the limb during the end of swing phase. Also in accordance with the function of retraction during the end of swing phase was the increased activity during the end of swing when mass was added to the wrists. Neither of these muscles was active during the support phase of the step when the dogs trotted at constant speed on a level treadmill. Both muscles were active during limb support, however, when the dogs ran uphill and when the dogs were pulled rearward by the experimenter. These observations suggest that the pectoralis profundus and latissimus dorsi muscles of dogs produce positive external work on the center of mass of the body during vigorous forward acceleration but are not involved in production of external work during constant-speed running. Both muscles displayed reduced activity during the end of swing phase when the dogs ran downhill and when the experimenter pulled the dog forward, suggesting that less muscular effort is required to end the swing phase when dogs are decelerating.

Adding mass to the trunk had little or no effect on the activity of the pectoralis profundus and the latissimus dorsi muscles, indicating that these muscles do not contribute to support of the

body against gravity. Pulling laterally on the trunk also did not influence the activity of these muscles, indicating that these muscles were not playing a role in mediolateral stabilization.

In summary, the pectoralis profundus and latissimus dorsi muscles of trotting dogs function to (1) brake and reverse the forward motion of the forelimb at the end of swing phase and (2) retract the forelimb during support phase to accelerate the dog forward when running uphill. Importantly, these muscles are not active during the support phase of the step when dogs run at constant speed trotting on a level treadmill. Previously, we reported similar results from a more cranial recording site in the pectoralis profundus (Carrier et al., 2006). Our findings of a lack of activity in the major forelimb retractor muscles during the support phase conflict with previous recordings from the latissimus dorsi muscle in Virginia opposums (Jenkins and Weijs, 1979), dogs (Tokuriki, 1973; Goslow et al., 1981) and cats (English, 1978). Our results are similar, however, to recordings made from a variety of primates during walking (Larson and Stern, 2007) and to recordings from the pectoralis profundus muscle in a dog made by Tokuriki (Tokuriki, 1973).

Omotransversarius muscle
The omotransversarius muscle of dogs protracts the forelimb during the beginning of swing phase and provides a protracting moment when dogs are actively decelerating in the forward direction. During constant-speed running on a level treadmill, the omotransversarius muscle is active during the last 30% of support and during the first half of swing phase, presumably to initiate swing phase. Adding mass to the wrists or running uphill each dramatically increased the activity of the muscle during this period, supporting the interpretation that the muscle functions to initiate swing phase. When the dogs ran downhill or were pulled forward by the experimenter, the muscle increased activity at the end of swing phase into early support phase, which is in accordance with a role in braking in the horizontal direction.

As was the case with the descending portion of the superficial pectoralis muscle, there was a trend towards increased activity at the very end of support phase when mass was added to the anterior trunk. This may be associated with the need to protract the limb more rapidly in swing phase.

Cleidobrachialis muscle
The cleidobrachialis muscle exhibited activity and responded to the force manipulations in ways that are consistent with the functions of protraction of the forelimb during the beginning of swing phase and production of a protraction moment during forward deceleration. The force manipulation that produced the most dramatic response from this muscle was the addition of mass to the wrists. In this case, activity increased during the end of support phase and beginning of swing phase, illustrating the muscle's role in protracting the forelimb early in swing phase. Increased activity in response to horizontal forces in all directions also suggests a role in stabilizing the trunk against horizontal perturbations.

Trapezius muscle
During a running step in mammals, the axis of rotation of the forelimb remains close to the dorsal margin of the spine of the scapula (Gray, 1968; Fischer et al., 2002). Thus, the anatomy of the cervical and thoracic portions of the trapezium muscle makes them ideally suited to stabilize the fulcrum of the forelimb in the fore/aft directions. The increase in activity of the cervical trapezius muscle during mid-stance when the dogs ran uphill or when the dogs were

pulled forward indicates a role of stabilizing of the fulcrum against forceful retraction of the forelimb. Similarly, the increased activity during the beginning of the swing phase in the thoracic trapezius when mass was added to the wrists is consistent with stabilization of the fulcrum against forceful protraction of the forelimb.

Strut-like behavior of the forelimb at the shoulder
Four of the muscles included in this analysis have anatomy appropriate to protract the forelimb: descending portion of the superficial pectoralis, omotransversarius, cleidobrachialis, and the cervical portion of the trapezius. Additionally, the thoracic portion of the trapezius is expected to stabilize the fulcrum of the forelimb during active protraction. When our dogs trotted at constant speed on a level treadmill, however, none of these muscles exhibited recruitment that is consistent with active protraction of the forelimb during limb support. A similar situation is true for the major forelimb retractor muscles. When the dogs trotted at constant speed on a level treadmill, the pectoralis profundus (present study) (Carrier et al., 2006) and the latissimus dorsi muscles were completely silent during limb support. The most likely explanation for these observations is that the ground force reaction vector is oriented at the fulcrum of the forelimb such that the forelimb functions as a strut at the shoulder (Gray, 1944; Gray, 1968; Carrier et al., 2006) when dogs trot at constant speed on level surfaces.

Another observation that supports the possibility that there is very little moment at the shoulder during constant-speed, level running is that adding mass to the anterior trunk produced little or no increase in the activity of the major protractor and retractor muscles. If there was a significant protraction or retraction moment on the forelimb during the support phase of a steady-state running step, adding mass to the trunk should increase that moment and elicit a large increase in the muscles that are responsible for the moment. Activity of these muscles did not increase substantially when mass was added to the anterior trunk. This is consistent with the ground reaction force vector being oriented so that it passes through, or very near, the fulcrum of the forelimb.

If the forelimb behaved as a strut at its attachment to the trunk, the work of running at constant speed would be accomplished not by the extrinsic forelimb muscles but by the muscles of the more distal joints: glenoid-humeral, elbow, wrist and metacarpo-phalangeal 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., 1998b; 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.

Integration of locomotion and ventilation
In addition to potentially reducing the cost of transport, minimizing the moments at the fulcrum of the forelimb during running at constant speed may also facilitate simultaneous running and breathing. Sustained vigorous locomotion characterizes mammals and is made possible, in part, by an ability to breathe during running (Bramble and Carrier, 1983; Carrier, 1987). If moments at the

shoulder are minimized, locomotor forces imposed on the trunk by the extrinsic forelimb muscles will also be minimized, 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).

During trotting, dogs display a variety of breathing patterns (Bramble and Carrier, 1983; Bramble and Jenkins, 1993; Carrier, 1996; Deban and Carrier, 2002; Ainsworth et al., 1989; Ainsworth et al., 1997). Once they are warmed up and pant to thermoregulate, however, they breathe in a stereotypic pattern of one breath per step. When breathing in this way, dogs tend to inhale during the first half of limb support phase and exhale during the second half of the step (Bramble and Jenkins, 1993; Carrier, 1996; Ainsworth et al., 1996). Many researchers have reasonably assumed that the phase relationships between ventilation and locomotor cycles in mammals and birds in some way minimize conflicting motions of the common musculo-skeletal elements (Bramble and Carrier, 1983; Young et al., 1992a; Young et al., 1992b; Bramble and Jenkins, 1993; Nassar et al., 2001; Deban and Carrier, 2002; Boggs, 1997; Boggs, 2002). Yet, in most or all cases, the mechanical basis of the coupled phase relationships remains unclear.

In the case of trotting dogs, the anatomy and activity of the extrinsic appendicular muscles associated with the swing phase of the forelimb may explain the observed phase relationship between ventilation and trotting. During the end of swing phase, the pectoralis profundus and the latissimus dorsi muscles are active to decelerate the forward motion of the forelimb and to initiate limb retraction. The pectoralis profundus muscle attaches to the sternum. The latissimus dorsi muscle attaches to the spinous processes of T6–L7 and the last two or three ribs. Thus, when these two retractor muscles turn on at the end of swing phase, they apply a cranially directed force on the sternum and caudal ribs, which could help initiate the beginning of inspiration. During the end of stance phase, the pectoralis superficialis transversus (Carrier et al., 2006) and pectoralis superficialis descendens muscles are active to initiate protraction of the forelimb in swing phase. Because these muscles originate from the cranial aspect of the sternum, their activity will exert a caudally directed force on the sternum that would likely facilitate expiratory airflow. Thus, when dogs trot at constant speed, the timing of inspiratory and expiratory airflow appears to be determined, at least partially, by the activity of the extrinsic muscles of the forelimb that produce the swing phase of the limb.

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