

Function of the extrinsic hindlimb muscles in trotting dogs

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SUMMARY

The extrinsic appendicular muscles of mammals have been suggested to impose parasagittal torques on the trunk that require recruitment of the oblique hypaxial muscles for stabilization. To determine if the recruitment of the protractors and retractors of the hindlimb are compatible with this hypothesis, we monitored changes in the recruitment of eleven muscles that span the hip joint to controlled manipulations of locomotor forces in trotting dogs. The results indicate that the primary retractor muscles of the hindlimb produce a small retraction moment at the hip joint early in the support phase during trotting at constant speed on a level surface. Thus, although the forelimb of dogs appears to function as a compliant strut, the hindlimb functions as a lever early in stance phase. Nevertheless, our results indicate that when dogs run at constant speed on a level surface a primary function of both the retractor and protractor muscles of the hindlimb is to produce swing phase of the limb. When the trotting dogs did net work in the fore–aft direction, by running uphill or downhill or by resisting a horizontally directed force, recruitment of the protractor and retractor muscles of the hip joint increased or decreased in the anticipated fashion. These observations are consistent with the hypothesis that recruitment of the oblique hypaxial muscles in trotting dogs function to stabilize the trunk against torques produced by protractor and retractor muscles of the hindlimb.

Key words: retractor muscles, protractor muscles, electromyogram, EMG, recruitment, quadruped, running, hip.

INTRODUCTION

Because the extrinsic appendicular muscles cross from attachment sites on the trunk to attachment sites on a limb, they play a central role in the mechanical integration of the limbs and trunk. In addition to the direct production of work at the proximal limb joints, these muscles can also serve to transfer energy from axial musculature to contribute to locomotor work. These functions require that the extrinsic limb muscles exert torques on both the limbs and trunk (Gray, 1968). It is these torques applied to the trunk, as well as those resulting from the inertia of the trunk itself as the body accelerates, that determine which axial muscles must be activated to provide postural stabilization of the trunk during a locomotor event.

Application of fore–aft directed forces on the ground requires that the extrinsic appendicular muscles apply torques on the trunk about the transverse axes through the limb girdles. Stabilization of the trunk against these torques has been suggested to require activity of the oblique hypaxial muscles (Fife et al., 2001). For example, during the application of a rearward-directed ground force (e.g. during acceleration) activity of the retractor muscles of the hindlimb exert a downward- and forward-directed force on the ischial tuberosity of the pelvis. This force applies a torque about the hip joint that acts to retrovert the pelvis. A torque with the opposite orientation is applied to the pelvis when the protractors of the hindlimb are active. These torques could be resisted by oblique hypaxial muscles. The internal oblique muscle attaches to the tuber coxae of the ilium, and its cranioventral orientation should allow it to stabilize the pelvis against the forces applied to the pelvis by the hindlimb retractor muscles. Similarly, the external oblique muscles have the correct architecture to resist the torques imposed on the trunk during deceleration in the forward direction (Fife et al., 2001). Nevertheless, fore–aft accelerations are small during constant speed

running and if the hindlimb behaves as a strut during running at constant speed, as is the case for the forelimb (Carrier et al., 2006), little or no torque would be applied at the hip joint during stance phase. If this were true, activity of the extrinsic appendicular muscles would not explain the observed patterns of hypaxial muscle activity.

In this investigation, we studied the locomotor function of the protractor and retractor muscles of the hindlimb of domestic dogs during trotting. Our objectives were to test whether or not recruitment of the protractors and retractors of the hindlimb is compatible with the hypothesis that the oblique hypaxial muscles stabilize the trunk against torques imposed by the extrinsic appendicular muscles, and to further characterize the locomotor function of the extrinsic hindlimb muscles in a mammalian cursor. We monitored changes in the recruitment of the protractor and retractor muscles in response to controlled manipulations of locomotor forces and moments. The rationale of the method is that changes in hindlimb mechanical requirements must be met by coincident changes in the recruitment of the muscles that transmit forces and moments between the hindlimb and the 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.

MATERIALS AND METHODS

Activity of eleven extrinsic appendicular muscles of the hindlimb was monitored in six mixed-breed dogs (*Canis lupus familiaris* Linnaeus 1758) while they trotted at moderate speed (approximately 2 m s^{-1}) on a motorized treadmill. Mean body mass of the six dogs was $25.1 \pm 3.0\text{ kg}$ (\pm s.d.). Each dog was obtained from a local animal shelter and trained to run on a treadmill. The muscles studied were the m. tensor fasciae latae, m. rectus femoris, cranial part of the m. sartorius, caudal part of the m. sartorius, cranial part of the m. biceps

femoris, caudal part of the m. biceps femoris, m. gluteus superficialis, m. gluteus medius, caudal belly of the m. semimembranosus, m. semitendinosus, m. gracilis, and the m. adductor magnus (Fig. 1). The anatomy of these muscles has been described by Evans (Evans, 1993). The study was carried out in parallel to recordings of the epaxial muscles (Schilling and Carrier, 2009) and therefore, the same experimental protocol and subjects were used in both studies. Surgical implantation of electrodes and recording were described in detail previously (Carrier et al., 2006). 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.

Locomotor force manipulations

To improve our understanding of the locomotor function of the eleven muscles, we monitored changes in the electromyogram (EMG) patterns of the muscles in response to manipulations of the locomotor forces. To increase the vertical forces on the hindlimbs, the dogs ran with a backpack containing mass of 0% (control), 8% and 12% of body mass. Although some inertial displacement of the added mass relative to the dog is unavoidable, the backpack held the added mass securely to the trunk of the dog, such that inertial movements of the mass were minimized. These were 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 elicit significant EMG responses from locomotor muscles. The masses were carried over the pelvic girdle (pelvic girdle mass). We attempted to place the added mass at the same relative location on the back of each dog directly above the acetabulum.

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 deg. (control), 10 deg. and 14 deg. 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. Conversely, when the dogs ran downhill, they did more negative (braking) work in the fore–aft direction. Dogs can traverse the inclines used (10 deg. and 14 deg.) with 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 forces by applying horizontally oriented forces directed forward and rearward on the dogs as they ran on a level treadmill. The application of these horizontal forces was probably equivalent in many ways to running on an incline. Although the applied load was not directed through the center of mass as it would be on an incline, and there were probably small differences in the placement of the feet under the body, these differences would almost certainly be small. Thus, we anticipated largely similar results from this manipulation and the hill running trials. 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 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 in line with the body axis. The applied force was monitored with a force transducer that was in-series with the leash. 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 hindlimbs during the swing phase of a running step, we added mass

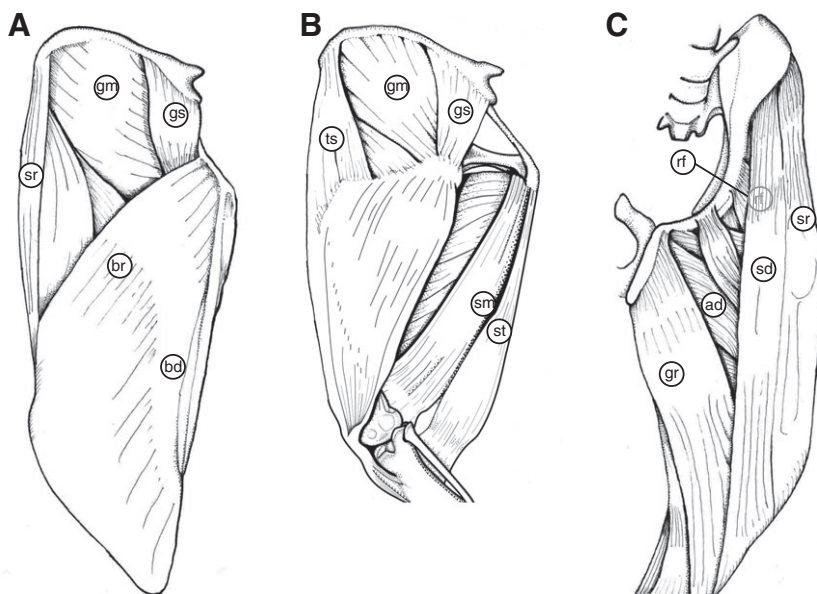


Fig. 1. Illustrations of the extrinsic appendicular muscles of the canid pelvic girdle, showing the location of the electrode placements used in this study. (A) Lateral view. (B) Lateral view with the m. biceps femoris removed. (C) Medial view.

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|------------------------------|-----------------------------|----------------------------|
| ad M. adductor magnus | gr M. gracilis | sm M. semimembranosus |
| bd M. biceps femoris caudal | gs M. gluteus superficialis | sr M. sartorius cranial |
| br M. biceps femoris cranial | rc M. rectus femoris | st M. semitendinosus |
| gm M. gluteus medialis | sd M. sartorius caudal | ts M. tensor fasciae latae |

of 0% (control), 1% and 2% of body mass to the dog's distal hindlimb around the tarsometatarsus (hindfoot mass). 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.

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 hindlimb support. The video recordings were used to identify the point in the accelerometer signal that represented touchdown and lift-off of the ipsilateral hindlimb. 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.

To illustrate the effects of the manipulations, the amplitude of EMGs was normalized to the average amplitude of the control trials. 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). 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. The results are presented graphically as median and the lower and upper quartile (e.g. Figs 2–5). Note that control and manipulation signals were plotted relative to the maximum amplitude observed in the respective manipulation. Thus, the relative amplitude of the control varies from figure to figure (e.g. Figs 3 and 4). The effect of the manipulation was also illustrated by plotting the difference between the control and manipulation signals as well as the 5th and the 95th quantile (Figs 2–5). Note that each difference trace was scaled to the maximum difference observed for that particular comparison. If error bars do not cross the x-axis, the difference between manipulation and control is statistically significant for that particular bin in the stride.

To determine whether or not a given force manipulation changed the recruitment of a muscle, the total rectified, integrated area of the manipulation EMG was divided by that of the control. If there was no effect of the manipulation, the result would be a ratio of 1. The effect of the manipulation was tested by comparing the mean ratio across dogs using the non-parametric Wilcoxon Sign-Rank 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 \pm 1 s.e.m. (e.g. Table 1).

To test if application of horizontally directed forces changed the recruitment of a given muscle, we used least squares, linear 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 (i.e. slope different from zero, P value < 0.05) of the normalized EMG area against normalized force with all dogs included in a single regression and calculated the Pearson product-moment correlation coefficient and the coefficient of determination (R^2).

RESULTS

In general, the force manipulations resulted in small or no changes in the periods of ipsilateral hindlimb support and swing phases (Carrier et al., 2006). In the steep downhill trials (14 deg.), 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 hindfoot mass trials, the duration of both support and swing phase was increased significantly. The swing phase of the 2% hindfoot mass trials was most dramatically affected, with a 26% increase in the period relative to the control trials.

M. tensor fasciae latae

When trotting at constant speed, the tensor fasciae latae muscle was active during the last 30% of ipsilateral hindlimb support (Fig. 2A, Fig. 3A, Fig. 4A, Fig. 5A). Activity began at roughly 70% of the support phase, increased to peak activity at 85% of support, declined rapidly and continued at a very low level into the beginning of ipsilateral swing phase, ending at approximately 40% of swing phase.

Adding mass to the trunk above the pelvic girdle increased the integrated activity of this muscle by 28% and 41% (Table 1). The increased activity was associated with the first half of ipsilateral swing phase rather than with the last third of support phase (Fig. 2A). When the dogs ran uphill, the mean activity increased by 1.83- and 2.49-fold above that observed during level trotting (Table 1). Activity was elevated during the last 20% of ipsilateral support phase and the first 30% of ipsilateral swing phase (Fig. 3A). When the subjects trotted downhill, mean activity of the tensor fasciae latae muscle decreased (Table 1). In contrast to the control trials, however, the muscle was active at a low level during much of ipsilateral support phase (Fig. 4A). Addition of mass to the distal hindlimb increased the activity of the tensor fasciae latae muscle by 1.7- and 2.1-fold (Table 1). The increased activity was most pronounced during the first 30% of ipsilateral swing phase (Fig. 5A). Of the two horizontal force

Table 1. Means of the integrated area of the electromyograms of the manipulated trials presented as a proportion of the control trials \pm standard error of change and number of individuals for the m. tensor fasciae latae, m. rectus femoris, m. sartorius cranial and m. sartorius caudal

Manipulation	Tensor	Rectus	SartCr	SartCd
Pelvic girdle mass				
8%	1.28 \pm 0.13 (6)*	3.01 \pm 0.54 (6)*	1.27 \pm 0.11 (6)*	1.36 \pm 0.16 (6)*
12%	1.41 \pm 0.14 (6)*	3.91 \pm 0.83 (6)*	1.42 \pm 0.13 (6)*	1.47 \pm 0.22 (6)*
Hills				
Uphill 10 deg.	1.83 \pm 0.16 (6)*	9.46 \pm 2.69 (6)*	1.94 \pm 0.23 (6)*	1.90 \pm 0.16 (6)*
Uphill 14 deg.	2.49 \pm 0.23 (6)*	13.53 \pm 2.69 (6)*	2.20 \pm 0.32 (6)*	2.14 \pm 0.20 (6)*
Downhill 10 deg.	0.61 \pm 0.11 (6)*	7.78 \pm 2.27 (6)*	0.82 \pm 0.15 (6)	0.73 \pm 0.08 (6)*
Downhill 14 deg.	0.91 \pm 0.15 (6)*	17.13 \pm 6.56 (6)*	1.29 \pm 0.27 (6)	1.02 \pm 0.10 (6)
Hindfoot mass				
1%	1.73 \pm 0.22 (6)*	5.39 \pm 1.53 (6)*	1.97 \pm 0.45 (6)*	1.17 \pm 0.20 (6)*
2%	2.12 \pm 0.37 (5)	14.58 \pm 4.11 (6)*	2.73 \pm 0.66 (6)*	1.87 \pm 0.14 (5)*

Tensor, m. tensor fasciae latae; Rectus, m. rectus femoris; SartCr, m. sartorius cranial; SartCd, m. sartorius caudal.

*Significant at $P < 0.05$; numbers in parentheses are the number of individuals.

manipulations, application of rearward-directed forces increased activity of the muscle, whereas application of forward-directed forces did not produce a significant effect (Table 2).

M. rectus femoris

During trotting on a level treadmill, the rectus femoris muscle exhibited two bursts of relatively low amplitude activity, the first burst occurring during the middle of ipsilateral support phase and the second occurring during the middle of ipsilateral swing phase (Fig. 2A, Fig. 3A, Fig. 4A, Fig. 5A). In some of the dogs, there was also a short low intensity burst of activity during the last 20% of support phase.

Addition of mass to the trunk increased the activity of the rectus femoris muscle by 3- and 3.9-fold (Table 1). Activity increased during the middle of ipsilateral swing phase (Fig. 2A). Running both uphill and downhill resulted in substantial increases in activity of the rectus femoris muscle (Table 1). When the dogs trotted uphill, activity increased 9- and 13-fold above the activity recorded during level trotting, with the greatest increase occurring during the middle

of ipsilateral support phase and a second smaller increase occurring during the middle of swing phase (Fig. 3A). By contrast, when the dogs trotted downhill, there was a large increase in activity during the beginning and middle of ipsilateral support phase (Fig. 4A). The increase in activity during downhill trotting was 7.8- and 17.1-fold (Table 1). The addition of mass to the distal hindlimb resulted in 5.4- and 14.6-fold increases in the activity of the rectus femoris muscle (Table 1). Increased activity was observed during the middle of ipsilateral support phase and the middle of swing phase (Fig. 5A). Activity of the rectus femoris muscle was positively correlated with horizontal forces applied in the forward and rearward directions (Table 2).

Cranial part of the m. sartorius

When the dogs trotted at constant speed on the level treadmill, the cranial part of the sartorius muscle exhibited a single burst of activity associated with the first half of ipsilateral swing phase (Fig. 2A, Fig. 3A, Fig. 4A, Fig. 5A). A very low level of activity was often observed during the last 15% of support phase. This low level activity continued into the beginning of swing phase and the primary burst of activity began at 10% and ended at 60% of ipsilateral swing phase.

Adding mass to the trunk increased the activity of the cranial portion of the sartorius muscle by 27% and 42% (Table 1). The increased activity occurred during the middle of ipsilateral swing phase (Fig. 2A). When the dogs trotted uphill, activity of this muscle increased 1.9- and 2.2-fold (Table 1). The increased activity was associated with the first half of ipsilateral swing phase, very similar in timing to the period of activity during level trotting (Fig. 3A). Although the integrated activity of the muscle did not change when the dogs trotted downhill (Table 1), the pattern of activity changed dramatically (Fig. 4A). During downhill trotting, activity during the first half of swing phase was dramatically reduced relative to level trotting, and the muscle exhibited a pronounced burst of activity during the first half of ipsilateral support phase, a burst not observed during level trotting. Adding mass to the distal hindlimb increased the activity of the cranial portion of the sartorius muscle 2- and 2.7-fold (Table 1). The increased activity was an amplification of the normal activity pattern observed when the dogs trotted in the control trials (Fig. 5A). The cranial portion of the sartorius muscle exhibited a positive correlation with horizontally applied force when the force was directed rearward and no correlation when the force was directed forward (Table 2).

Table 2. Relationship between applied horizontal forces and EMG area for the extrinsic appendicular muscles of the hindlimb for all dogs

Muscle	Forward pull		Backward pull	
	Slope (R^2)/ P value		Slope (R^2)/ P value	
M. tensor fasciae latae	-0.09 (0.01)	0.1541	0.28 (0.09)	<0.0001*
M. rectus femoris	0.53 (0.37)	<0.0001*	0.45 (0.28)	<0.0001*
M. sartorius cranial	0.04 (0.00)	0.4454	0.25 (0.09)	<0.0001*
M. sartorius caudal	0.01 (0.00)	0.9170	0.33 (0.15)	<0.0001*
M. gluteus superficialis	-0.02 (0.00)	0.8013	0.56 (0.36)	<0.0001*
M. gluteus medius	-0.41 (0.20)	<0.0001*	0.63 (0.55)	<0.0001*
M. semimembranosus	-0.41 (0.25)	<0.0001*	0.62 (0.40)	<0.0001*
M. biceps femoris cranial	-0.20 (0.06)	0.0007*	0.74 (0.62)	<0.0001*
M. biceps femoris caudal	0.13 (0.02)	0.0599	0.30 (0.46)	<0.0001*
M. gracilis	0.13 (0.02)	0.0395*	0.52 (0.34)	<0.0001*
M. semitendinosus	4.82 (0.69)	<0.0001*	0.59 (0.36)	<0.0001*
M. adductor magnus	0.01 (0.00)	0.8668	0.38 (0.21)	<0.0001*

During the forward pull, the dog was pulled forward *via* the muzzle, i.e. the dogs pushed backwards to counteract the applied forces. During the backward pulls, the dog was pulled backwards *via* the harness, i.e. the dogs pulled forward.

*Significant at $P < 0.05$.

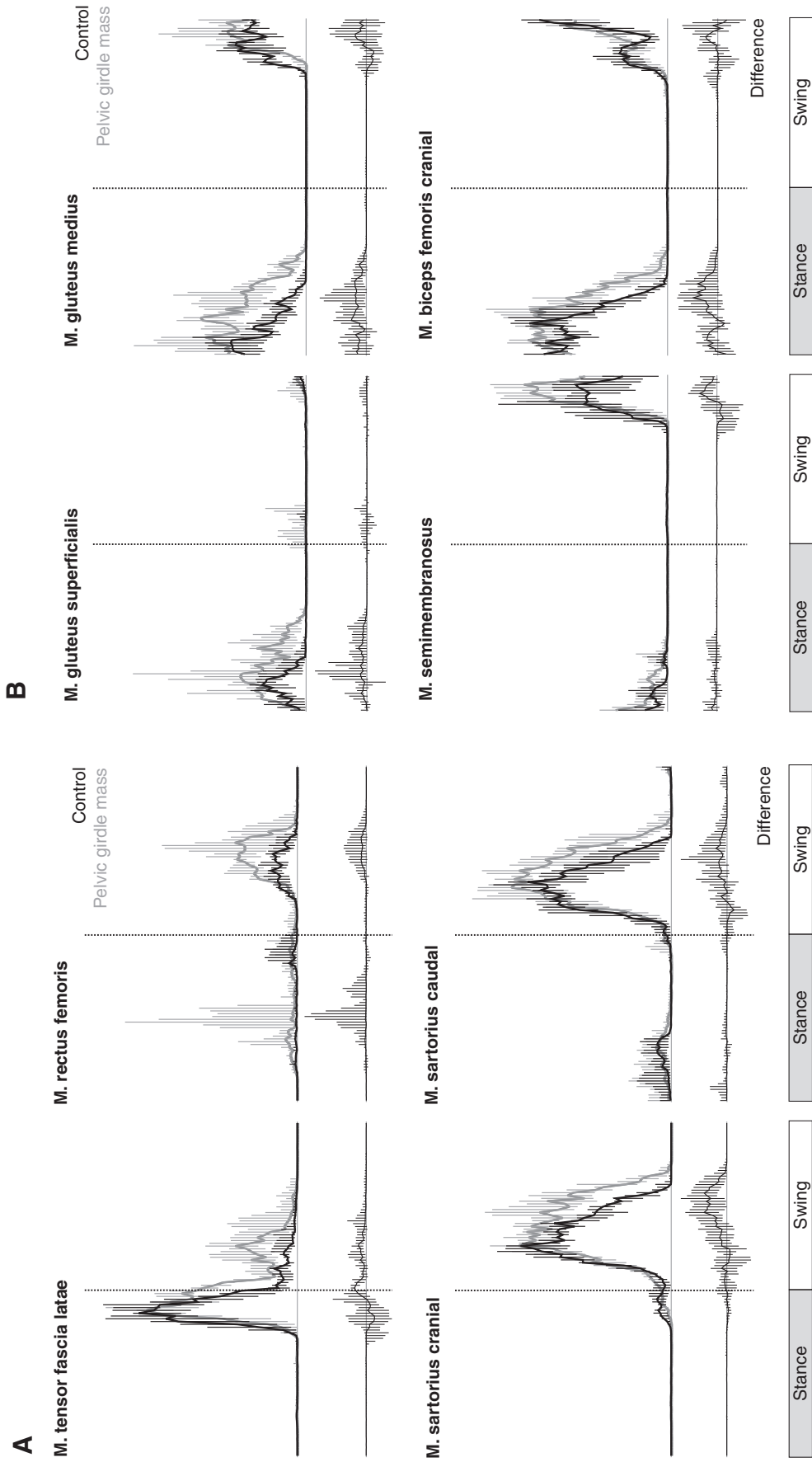
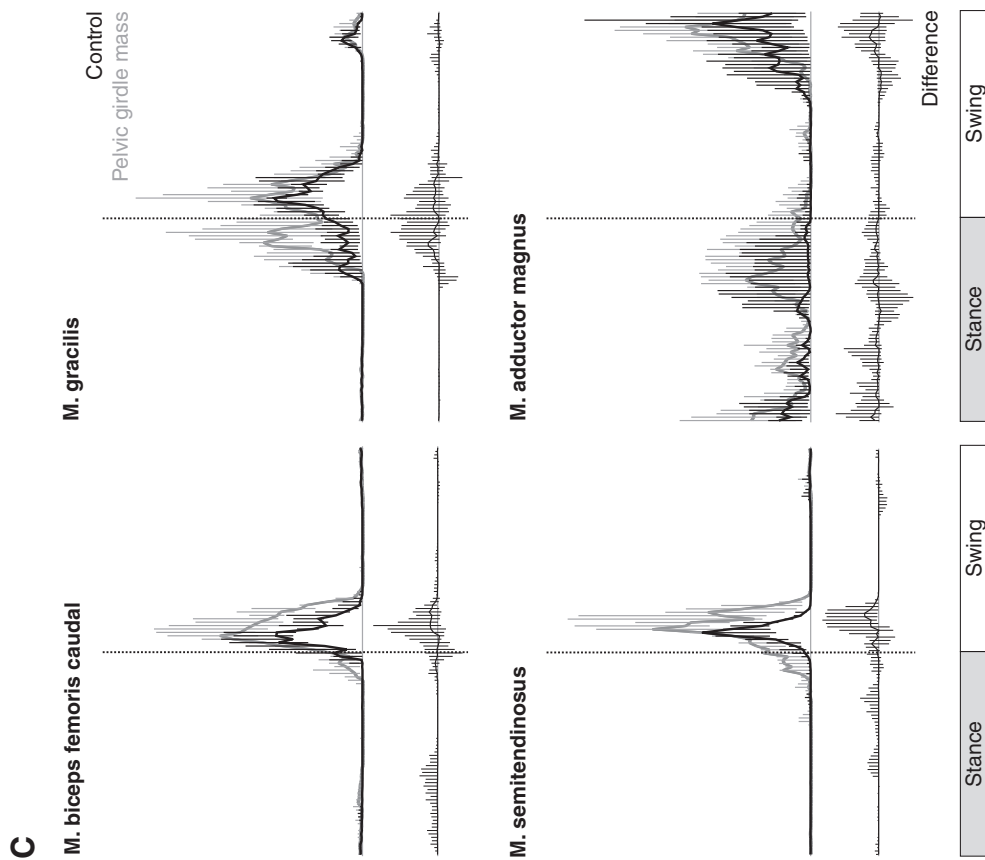


Fig. 2. See next page for legend.

Fig. 2. Normalized EMGs for control and manipulation signals as well as the difference between control and manipulation trials from all six dogs when they trotted with 12% of their body mass carried in a backpack located over their pelvic girdle. (A) *M. tensor fasciae latae*, *m. rectus femoris*, cranial and caudal parts of the *m. sartorius*. (B) *M. gluteus superficialis*, *m. gluteus medius*, *m. semimembranosus*, cranial part of *m. biceps femoris*. (C) The caudal part of *m. biceps femoris*, *m. gracilis*, *m. semitendinosus*, *m. adductor magnus*. The x-axis shows the ipsilateral hindlimb stance (left) and swing (right). For each dog, the trotting speed was the same during the control and experimental trials. Normalized EMG: the black line represents the median of the averaged EMGs when the dogs trotted on the level without added mass (control); the gray line represents the median of the averaged EMG when the dogs carried the added mass. The error bars represent the upper and lower quartile for each bin. Note that control and manipulation signals were plotted relative to the maximum amplitude observed in the particular manipulation experiment. Difference: median as well as the 5th and the 95th quantile of the difference between the control and the manipulation signal on a bin-by-bin basis for all dogs. Negative values indicate that the manipulation signal was decreased relative to the control; positive values indicate that the manipulation signal was increased relative to the control. Control and manipulation signals per bin are significantly different when the error bars do not contact the x-axis. Note that these traces were plotted relative to the maximum difference observed for the given sampling site to optimally present the difference. The difference traces are therefore not directly comparable among sampling sites.



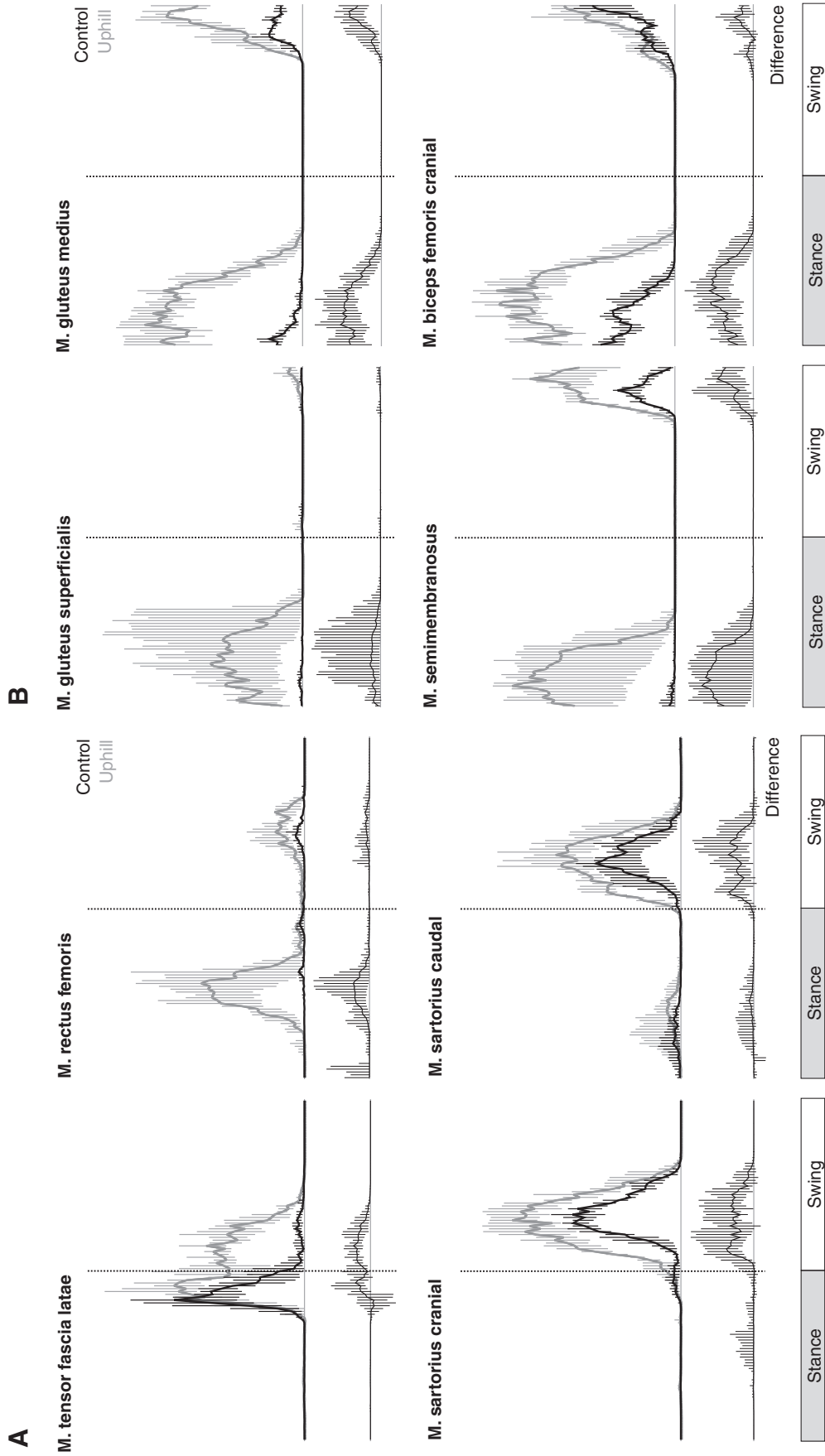
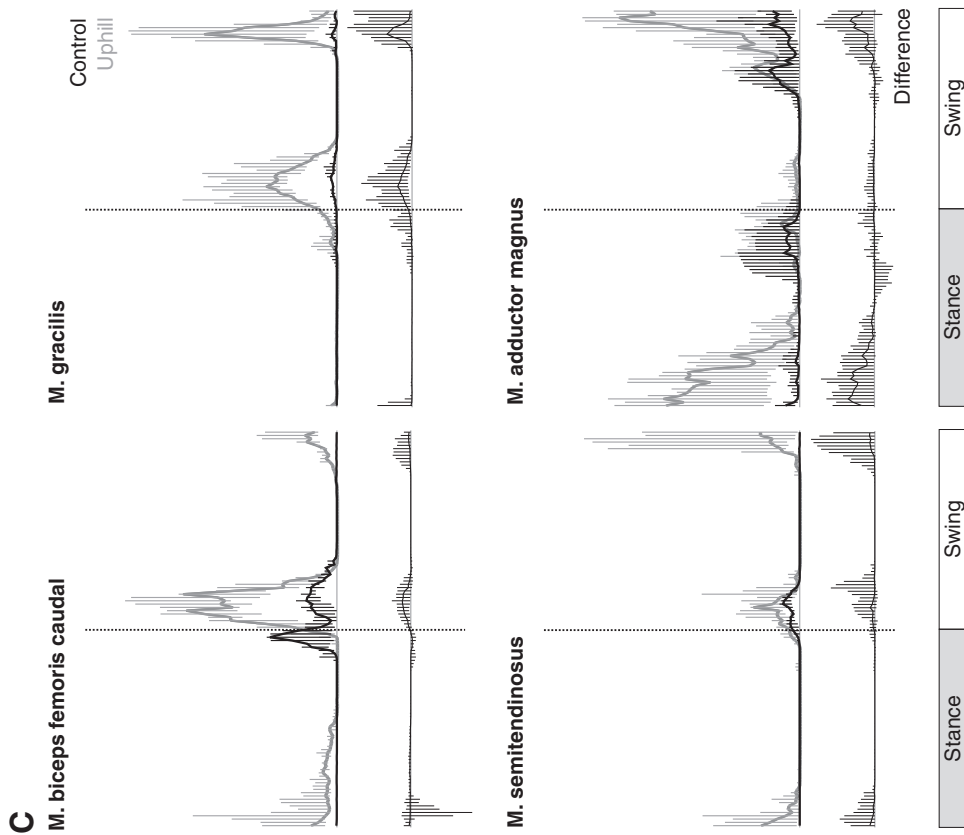


Fig. 3. See next page for legend.

Fig. 3. Normalized EMGs for control and manipulation signals as well as the difference between control and manipulation trials from all six dogs when they trotted uphill (14 deg.). (A) *M. tensor fasciae latae*, *m. rectus femoris*, cranial and caudal parts of the *m. sartorius*. (B) *M. gluteus superficialis*, *m. gluteus medius*, *m. semimembranosus*, cranial part of *m. biceps femoris*. (C) The caudal part of *m. biceps femoris*, *m. gracilis*, *m. semitendinosus*, *m. adductor magnus*. See Fig. 2 for further explanation.



Caudal part of the m. sartorius

The caudal portion of the sartorius muscle exhibited two bursts of activity when the dogs trotted on a level treadmill (Fig. 2A, Fig. 3A, Fig. 4A, Fig. 5A). A relatively small burst of activity was observed during the first half of ipsilateral support phase and a much larger burst of activity occurred during the first half of swing phase. The activity during swing phase was very similar in timing to the activity observed for the cranial portion of the sartorius muscle.

This muscle's responses to the various force manipulations were virtually the same as those observed for the cranial portion of the muscle (Table 1). Adding mass to the trunk increased the activity, primarily during the middle of ipsilateral swing phase (Fig. 2A). Running uphill increased the activity dramatically during the first half of swing phase (Fig. 3A), whereas running downhill resulted in decreased activity during swing phase (Fig. 4A). Adding mass to the distal hindlimbs increased the integrated activity (Table 1), but the variation among the dogs was such that the result was not significant on a bin-by-bin basis (Fig. 5A). The caudal portion of the sartorius muscle exhibited a positive correlation with applied horizontal force when the force was directed rearward and no correlation when the force was applied in the forward direction (Table 2).

M. gluteus superficialis

When the dogs trotted on the level treadmill, the gluteus superficialis muscle exhibited two bursts of relatively low-level activity (Fig. 2B, Fig. 3B, Fig. 4B, Fig. 5B). The larger burst occurred during the last 20% of ipsilateral swing phase and the first third of ipsilateral support phase. The smaller burst was observed during the first 20% of swing phase.

Adding mass to the trunk tended to increase the activity of the superficial gluteus muscle 2.3- and 2.5-fold (Table 3). The increased activity occurred during the first half of ipsilateral support phase (Fig. 2B). Trotting uphill resulted in dramatic 22- and 37-fold increases in the activity of the superficial gluteus muscle compared with level trotting (Table 3). Activity during uphill trotting was largely restricted to the first two-thirds of ipsilateral support phase (Fig. 3B). Trotting downhill did not produce a significant change in the integrated activity of this muscle (Table 3, Fig. 4B). Adding mass to the distal hindlimb resulted in dramatic 8.5- and 16.7-fold increases in the activity of the superficial gluteus muscle (Table 3). The increased activity occurred during the first 30% of support phase (Fig. 4B). The

rearward-directed horizontal forces were positively correlated with the activity of the superficial gluteus muscle (Table 2). Application of horizontal force from the forward direction did not produce significant changes in the activity of this muscle.

M. gluteus medius

The medial gluteus muscle was active in a single burst during the last third of ipsilateral swing phase and approximately the first 40% of support phase when the dogs trotted on the level treadmill (Fig. 2B, Fig. 3B, Fig. 4B, Fig. 5B).

Addition of mass to the trunk increased activity of the medial gluteus muscle by 56% and 69% (Table 3). The increase occurred during the first half of ipsilateral support phase (Fig. 2B). Trotting uphill produced 6.3- and 7.4-fold increases in activity of the medial gluteus muscle (Table 3). Activity occurred during the last third of ipsilateral swing phase and the first 60% of support phase (Fig. 3B). By contrast, trotting downhill resulted in dramatic 6.7- and 8.3-fold decreases in activity of the medial gluteus muscle relative to control trials (Table 3, Fig. 4B). Adding mass to the distal hindlimb resulted in 2.0- and 2.9-fold increases in activity of the medial gluteus muscle (Table 3). In these trials, the muscle was active during the last 30% of swing phase and the first 50% of support phase, with the greatest increase in activity relative to controls occurring during the first half of support phase (Fig. 5B). Application of horizontally oriented force yielded a significant positive correlation between muscle activity and rearward-directed force, and a negative correlation between muscle activity and forward-directed forces (Table 2).

M. semimembranosus

When the dogs trotted on the level treadmill, the semimembranosus muscle was active primarily during the last third of ipsilateral swing phase (Fig. 2B, Fig. 3B, Fig. 4B, Fig. 5B). The muscle became active at 70% of swing phase, reached peak activity late in swing phase, and then activity declined rapidly and continued at a much lower level through the first 30% of ipsilateral support phase.

Adding mass to the trunk increased the activity of the semimembranosus muscle by 29% and 26% (Table 3). The increased activity was associated with the last 20% of ipsilateral swing phase and the first half of ipsilateral support phase (Fig. 2B). Activity of the semimembranosus muscle increased 6.5- and 7.7-fold when the dogs trotted uphill (Table 3). The increase occurred during both the end of ipsilateral swing phase and the first half of support phase

Table 3. Means of the integrated area of the electromyograms of the manipulated trials presented as a proportion of the control trials \pm standard error of change for m. gluteus superficialis, m. gluteus medius, m. semimembranosus and m. biceps femoris cranial

Manipulation	GlutSup	GlutMed	Membr	BicCr
Pelvic girdle mass				
8%	2.32 \pm 0.52 (6)*	1.56 \pm 0.13 (6)*	1.29 \pm 0.11 (6)*	1.17 \pm 0.04 (6)*
12%	2.47 \pm 0.42 (6)*	1.69 \pm 0.18 (6)*	1.26 \pm 0.11 (6)*	1.31 \pm 0.04 (6)*
Hills				
Uphill 10 deg.	22.19 \pm 9.51 (6)*	6.32 \pm 0.58 (6)*	6.47 \pm 1.68 (6)*	2.77 \pm 0.20 (6)*
Uphill 14 deg.	37.51 \pm 19.80 (6)*	7.38 \pm 0.65 (6)*	7.68 \pm 1.81 (6)*	3.17 \pm 0.22 (6)*
Downhill 10 deg.	1.90 \pm 1.04 (6)	0.15 \pm 0.09 (6)*	0.20 \pm 0.04 (6)*	0.58 \pm 0.07 (6)*
Downhill 14 deg.	1.37 \pm 0.67 (6)	0.12 \pm 0.07 (6)*	0.21 \pm 0.04 (6)*	0.68 \pm 0.07 (6)*
Hindfoot mass				
1%	8.50 \pm 4.48 (6)*	1.98 \pm 0.32 (6)*	1.52 \pm 0.30 (6)*	1.30 \pm 0.07 (6)*
2%	16.72 \pm 8.29 (5)*	2.88 \pm 0.42 (5)*	2.34 \pm 0.33 (6)*	1.79 \pm 0.18 (5)*

GlutSup, m. gluteus superficialis; GlutMed, m. gluteus medius; Membr, m. semimembranosus; BicCr, m. biceps femoris cranial.

*Significant at $P < 0.05$; numbers in parentheses are the number of individuals.

Table 4. Means of the integrated area of the electromyograms of the manipulated trials presented as a proportion of the control trials \pm standard error of change for m. biceps femoris caudal, m. gracilis, m. semitendinosus and m. adductor magnus

Manipulation	BicCd	Grac	Tend	Add
Pelvic girdle mass				
8%	1.51 \pm 0.35 (5)	1.68 \pm 0.30 (6)*	1.69 \pm 0.41 (5)	1.32 \pm 0.14 (6)*
12%	2.00 \pm 0.68 (5)*	1.82 \pm 0.40 (6)*	2.54 \pm 0.76 (5)*	1.37 \pm 0.15 (6)*
Hills				
Uphill 10 deg.	1.95 \pm 0.43 (5)*	9.62 \pm 3.17 (6)*	6.79 \pm 3.16 (5)*	2.21 \pm 0.53 (5)*
Uphill 14 deg.	2.59 \pm 0.66 (5)*	14.10 \pm 5.07 (6)*	10.81 \pm 4.93 (5)*	2.68 \pm 0.73 (5)*
Downhill 10 deg.	0.70 \pm 0.18 (5)	0.48 \pm 0.17 (6)*	1.30 \pm 0.48 (5)	0.86 \pm 0.25 (5)
Downhill 14 deg.	1.26 \pm 0.48 (5)	0.78 \pm 0.47 (6)*	1.19 \pm 0.49 (5)	0.78 \pm 0.27 (5)
Hindfoot mass				
1%	3.25 \pm 0.92 (5)*	9.08 \pm 3.39 (6)*	14.77 \pm 8.33 (5)*	1.27 \pm 0.10 (6)*
2%	5.20 \pm 0.90 (4)	17.01 \pm 6.74 (5)*	20.73 \pm 12.03 (5)*	1.53 \pm 0.22 (5)*

BicCd, m. biceps femoris caudal; Grac, m. gracilis; Tend, m. semitendinosus; Add, m. adductor magnus.

*Significant at $P < 0.05$; numbers in parentheses are the number of individuals.

(Fig. 3B). By contrast, when the dogs trotted downhill, activity of this muscle decreased 5.0-fold, and no activity occurred during support phase (Fig. 4B). Addition of mass to the distal hindlimb increased the activity of the semimembranosus muscle 1.5- and 2.3-fold above control values (Table 3). The increased activity was associated with the first half of support phase (Fig. 4B). Activity of the semimembranosus muscle exhibited a positive correlation with applied rearward-directed horizontal force and a negative correlation with forward-directed horizontal forces (Table 2).

Cranial portion of the m. biceps femoris

During trotting on the level treadmill, the cranial portion of the biceps femoris muscle was active in a single burst during the last third of ipsilateral swing phase and the first 30–40% of ipsilateral support phase (Fig. 2B, Fig. 3B, Fig. 4B, Fig. 5B). Starting late in swing phase, activity increased gradually to maximum levels early in support phase.

Adding mass to the trunk increased activity of the muscle by 12% and 31% above control values (Table 3). The increased activity was associated with the first half of support phase rather than with the end of swing phase (Fig. 2B). Running uphill elicited large increases in activity, of 2.7- and 3.2-fold, in the cranial portion of the biceps femoris muscle (Table 3). Activity was elevated relative to level trotting during the last part of ipsilateral swing phase and dramatically increased during the first 65% of ipsilateral support phase (Fig. 3B). By contrast, activity of this muscle decreased when the dogs ran downhill (Table 3). The largest decrease occurred during the first third of ipsilateral support phase (Fig. 4B). Activity of the cranial portion of the biceps femoris increased when mass was added to the distal hindlimb (Table 3). The increased activity occurred throughout the normal activity period, but was not significant on a bin-by-bin basis (Fig. 5B). The cranial portion of the biceps femoris muscle exhibited a positive correlation with rearward-directed horizontally applied forces and a negative correlation when the force was directed forward (Table 2).

Caudal portion of the m. biceps femoris

The caudal portion of the biceps femoris muscle was active during the beginning of ipsilateral swing phase when the dogs trotted on the level treadmill (Fig. 2C, Fig. 3C, Fig. 4C, Fig. 5C). Activity began shortly before the end of support phase and continued for the first 20% of swing phase.

Adding mass to the trunk tended to increase the activity of the caudal portion of the biceps femoris but the increase was

significantly in only the 12% trials (Table 4). The increased activity occurred during the first 20% of ipsilateral swing phase, the same period of activity was observed during level trotting (Fig. 2C). When the dogs trotted uphill, activity of the caudal portion of the biceps femoris muscle increased by 2- and 2.6-fold (Table 4). Activity was elevated during the beginning of ipsilateral swing phase and a second burst of activity was observed during the end of swing phase and the first half of ipsilateral support phase (Fig. 3C). Trotting downhill did not change the integrated activity of this portion of the biceps femoris muscle (Table 4). Nevertheless, on a bin-by-bin basis activity was reduced during the beginning of swing phase when the dogs trotted downhill (Fig. 4C). Adding mass to the distal hindlimb tended to increase the activity of the caudal biceps femoris muscle (Table 4). Activity began much earlier in support phase and remained elevated during the end of support phase (Fig. 5). The caudal portion of the biceps femoris muscle exhibited a positive correlation with horizontally applied force when the force was directed rearward (Table 2). The forward-directed forces were not correlated with the activity of this muscle.

M. gracilis

When the dogs trotted on the level treadmill, the gracilis muscle was active at a low level during the last third of ipsilateral support phase and the first third of swing phase (Fig. 2C, Fig. 3C, Fig. 4C, Fig. 5C). A smaller burst of activity was also observed at the end of ipsilateral swing phase.

Activity of the gracilis muscle increased by 68% and 82% when the dogs carried additional mass over their pelvic girdles (Table 4). The increased activity occurred during the same activity period as observed for the unloaded control trials (Fig. 2C). The other trunk weight manipulations did not yield significant differences from the control trials. Trotting uphill resulted in dramatic 9.6- and 14.1-fold increases in activity of the gracilis muscle although only the 10 deg. incline trial result was significantly different from the level control trials (Table 4). During the uphill trials, activity of the gracilis muscle occurred primarily in two bursts, during the first third of ipsilateral swing phase and the last 20% of swing phase (Fig. 3C). When the dogs trotted downhill, activity of this muscle decreased (Table 4, Fig. 4C). Adding mass to the distal hindlimb resulted in dramatic 9- and 17-fold increases in the activity of the gracilis muscle above the activity recorded in the unloaded trials (Table 4). Activity of the gracilis muscle in these trials occurred mainly in a single burst starting midway through ipsilateral support phase and ending at 30% of swing phase (Fig. 5C). Activity of the gracilis muscle exhibited

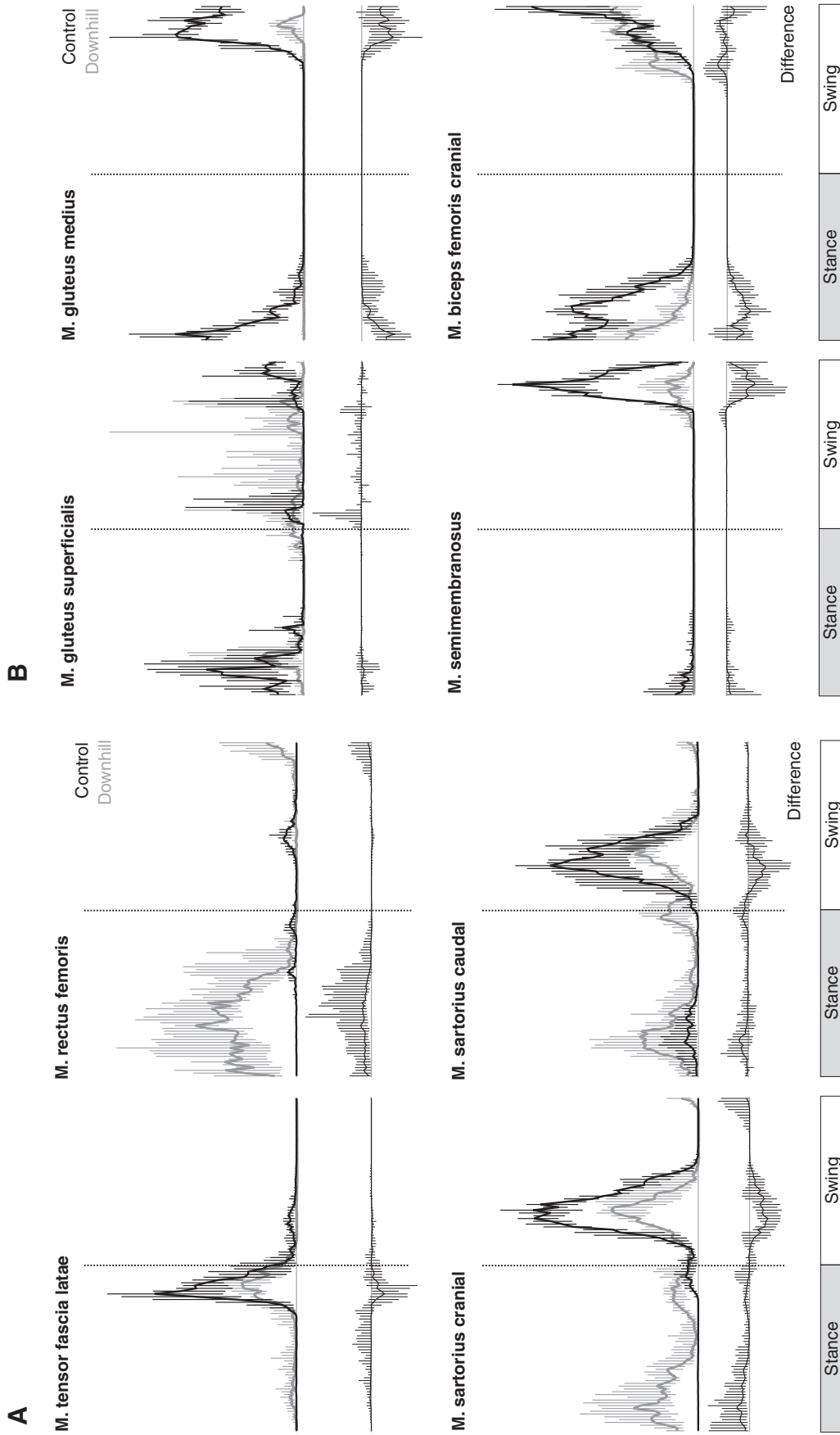
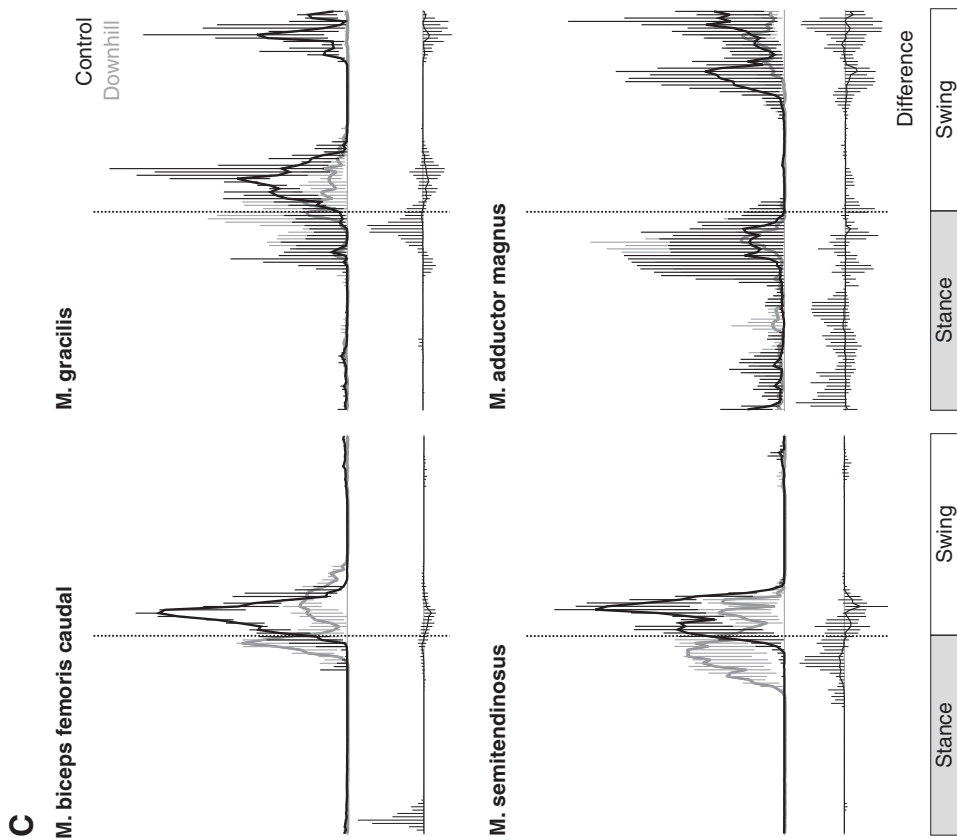


Fig. 4. See next page for legend.

Fig. 4. Normalized EMGs for control and manipulation signals as well as the difference between control and manipulation trials from all six dogs when they trotted downhill (14 deg.). (A) M. tensor fasciae latae, m. rectus femoris, cranial and caudal parts of the m. sartorius. (B) M. gluteus superficialis, m. gluteus medius, m. semimembranosus, cranial part of m. biceps femoris. (C) The caudal part of m. biceps femoris, m. gracilis, m. semitendinosus, m. adductor magnus. See Fig. 2 for further explanation.



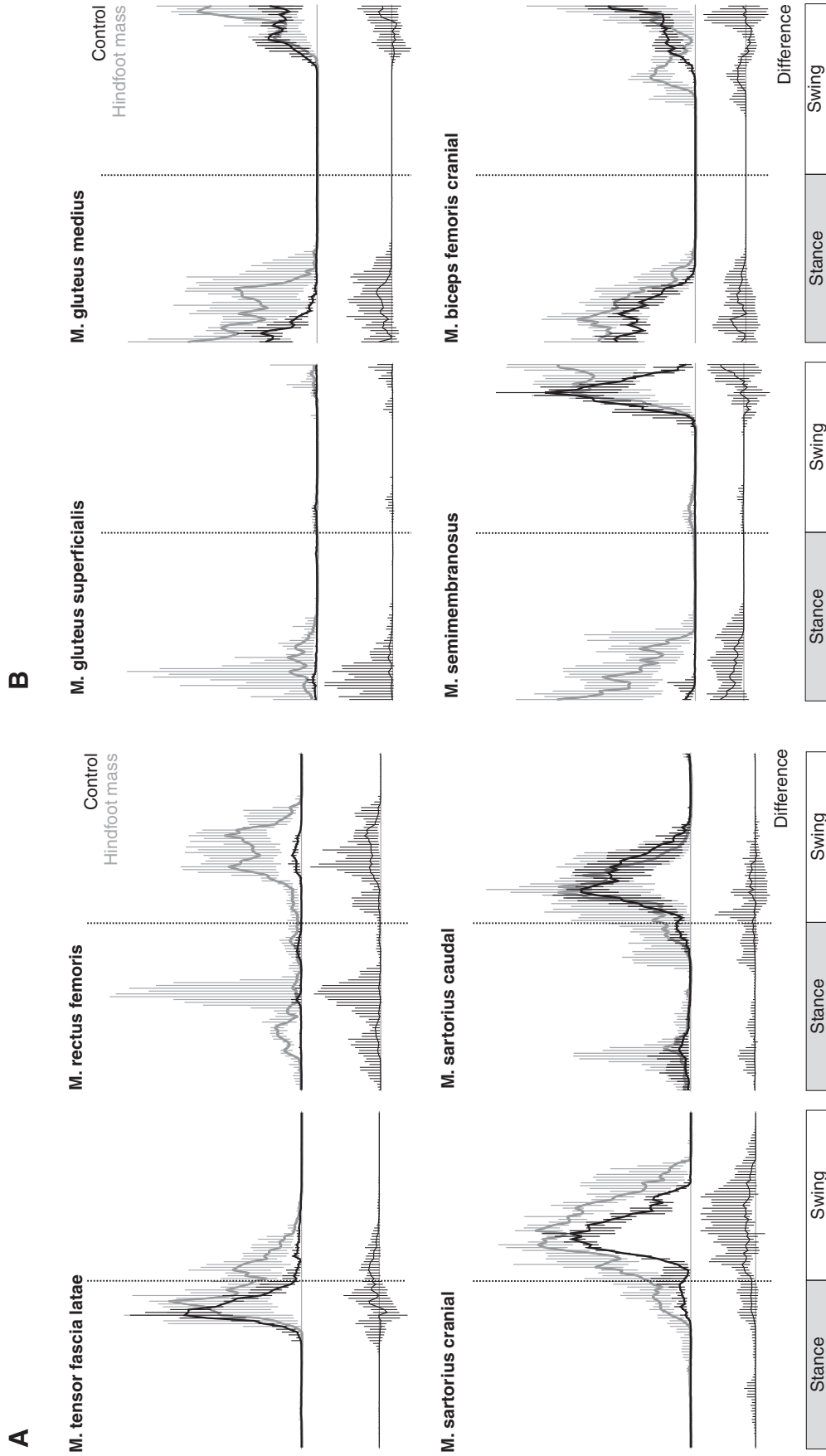
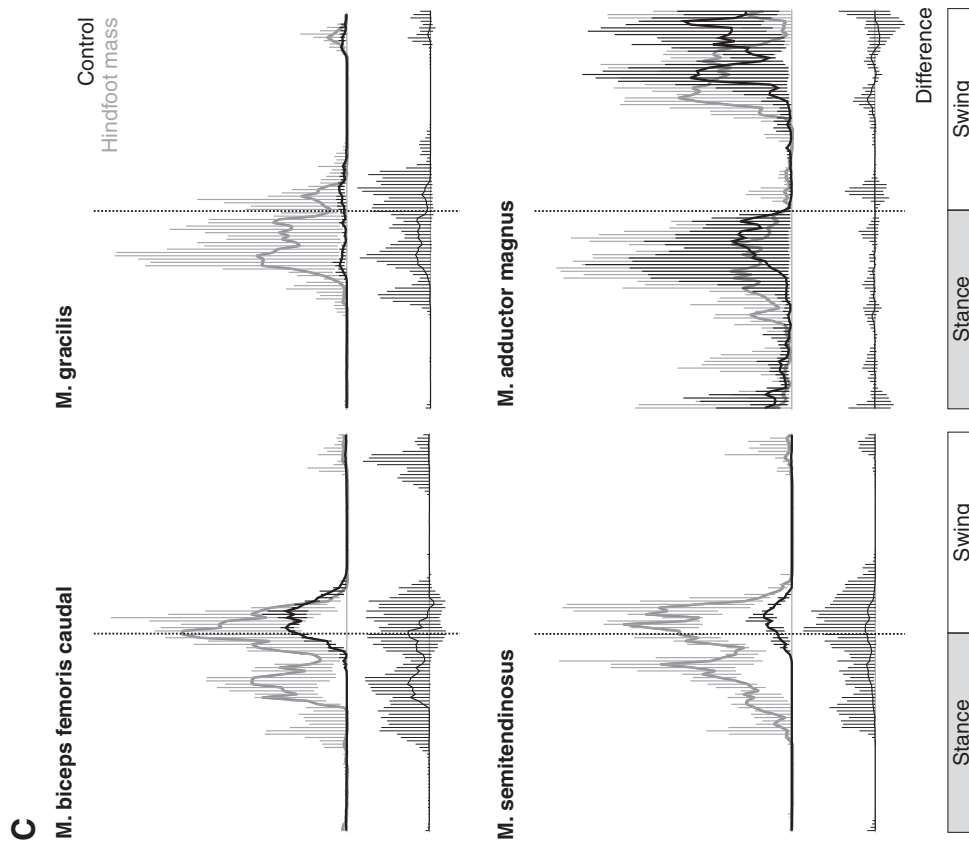


Fig. 5. See next page for legend.

Fig. 5. Normalized EMGs for control and manipulation signals as well as the difference between control and manipulation trials from all six dogs when they trotted with 2% of their body mass added to their hindlimbs. (A) *M. tensor fasciae latae*, *m. rectus femoris*, cranial and caudal parts of the *m. sartorius*. (B) *M. gluteus superficialis*, *m. gluteus medius*, *m. semimembranosus*, cranial part of *m. biceps femoris*. (C) The caudal part of *m. biceps femoris*, *m. gracilis*, *m. semitendinosus*, *m. adductor magnus*. See Fig. 2 for further explanation.



a positive correlation with applied rearward-directed horizontal force and a weak positive correlation with forward-directed horizontal forces (Table 2).

M. semitendinosus

When the dogs trotted on the level treadmill, the semitendinosus muscle was active during the first 20% of ipsilateral swing phase (Fig. 2C, Fig. 3C, Fig. 4C, Fig. 5C). Activity often began at a low level shortly before the end of ipsilateral support phase, and then increased dramatically at the initiation of swing phase.

Addition of mass to the trunk tended to increase the activity of the semitendinosus muscle, but only in the 12% pelvic girdle mass trials were the results significantly different from the unloaded control trials (Table 4). The increased activity occurred during the first third of ipsilateral swing phase (Fig. 2C). Trotting uphill greatly increased the integrated activity of the semitendinosus muscle, by 6.8- and 10.8-fold (Table 4). Activity was increased during the beginning of ipsilateral swing phase as well as during the end of swing phase and the beginning of support phase (Fig. 3C). Trotting downhill did not change the integrated activity of this muscle (Table 4). However, on a bin-by-bin basis, the activity increased during the end of support phase and decreased during the beginning of swing phase (Fig. 4C). Adding mass to the distal hindlimb resulted in large, 14.7- and 20.7-fold increases of the semitendinosus muscle (Table 4). The period of activity when mass was added to the distal hindlimb began halfway through ipsilateral support phase and ended at 30% of swing phase (Fig. 5C). Activity of the semitendinosus muscle exhibited positive correlations with applied rearward- and forward-directed horizontal forces (Table 2).

M. adductor magnus

The adductor magnus muscle exhibited two bursts of activity when the dogs trotted on the level treadmill, one during the second half of ipsilateral support phase and one during the second half of swing phase (Fig. 2C, Fig. 3C, Fig. 4C, Fig. 5C).

When the dogs carried additional mass on their trunk, activity of the adductor magnus muscle increased by 32% and 37% (Table 4). This increase, however, was not significant on a bin-by-bin basis (Fig. 2C). Trotting uphill increased the activity of the adductor magnus muscle 2.2- and 2.7-fold over the level control trials (Table 4). The increased activity occurred during the last 30% of ipsilateral swing phase and the first 40% of support phase (Fig. 3C). Trotting downhill was associated with non-significant decreases in activity of this muscle (Table 4, Fig. 4C). Adding mass to the distal hindlimb resulted in no change in the activity of the semitendinosus muscle (Table 4, Fig. 5C). Activity of the adductor magnus muscle was correlated with the rearward-directed horizontal forces but not the forward-directed forces (Table 2).

DISCUSSION

Protraction and retraction of the hindlimb is accomplished by three groups of extrinsic appendicular muscles. (1) Muscles that function primarily to retract the hindlimb at the hip joint include the cranial portion of the biceps femoris, superficial gluteus, medial gluteus, semimembranosus, and possibly the adductor magnus. (2) Muscles that can function to retract the hindlimb but also cross and can flex the knee joint include the caudal part of the biceps femoris, semitendinosus and the gracilis muscles. (3) Muscles that protract the hindlimb include the tensor fasciae latae muscle, both heads of the sartorius muscle, and possibly the rectus femoris muscle.

Primary retractors of the hindlimb

During trotting on a level treadmill, four of the primary retractor muscles of the hip, cranial portion of the biceps femoris, superficial gluteus, medial gluteus and semimembranosus, exhibited a single, relatively low-level burst of activity that began late in ipsilateral swing phase and continued through the first third of support phase. The activity periods of the gluteus medius and cranial portion of the biceps femoris muscles in trotting dogs (Goslow et al., 1981) and horses (Robert et al., 1999) are virtually identical to those reported here. Trotting cats also exhibit similar recruitment of these two extensor muscles but with a somewhat longer period of activity during the support phase (Rasmussen et al., 1978). The semimembranosus muscle of cats, however, differs from the pattern reported here and previously for dogs (Gregersen et al., 1998), in displaying bursts of activity during both swing and stance phases (Rasmussen et al., 1978). Activity of the primary hip retractor muscles of trotting rats also differ from dogs in that the gluteus medius muscle of rats has a burst of activity during both swing and stance phases and the semimembranosus muscle is active during the second half of stance rather than the first half (Nicolopoulos-Stournaras and Iles, 1984).

Recruitment of the primary hip retractor muscles early in support phase when dogs trot on a level surface indicates that the hindlimb acts as a lever early in stance, as suggested by Gray (Gray, 1944; Gray, 1968). This finding is consistent with an analysis of the gear ratio at the hip of dogs that indicated a positive retractor moment at the hip during the first 40% of support phase of a trotting step (Carrier et al., 1998). Activity from these primary retractor muscles during trotting distinguishes the hindlimb of dogs from the forelimb in which the retractor muscles are not active during the support phase (Carrier et al., 2006; Carrier et al., 2008). Thus, although the forelimb of dogs functions as a compliant strut during running at constant speed on level surfaces, the hindlimb functions as a lever early in stance phase.

Adding mass to the trunk can increase protractor and retractor moments at the hip joint. During rapid acceleration and deceleration of the center of mass of the body, running animals must exert shearing (i.e. horizontal) forces on the ground with their hindlimbs. These forces often result in ground force reaction vectors that are not directed at the hip joint (Lee et al., 1999; Aerts et al., 2003; Roberts and Scales, 2004; Gregersen and Carrier, 2004; McGowan et al., 2005). If the ground reaction force vector is not directed at the hip joint, but is positioned in front or behind it, extrinsic muscles must be active to support the animal's body weight; the alternative is collapse of the body at the hip joint. Thus, if during the support phase of a running step there is a significant retraction moment on the hindlimb, adding mass to the trunk will increase that moment and can be expected to elicit an increase in the activity of the muscles that are responsible for the moment. Therefore, the observation that activity of all five primary retractor muscles increased when additional mass was carried over the pelvic girdle during trotting is consistent with the hypothesis that the hindlimb functions as a lever during trotting on level surfaces.

The primary retractor muscles exhibited substantial, 2.2- to 22-fold, increases in activity when the dogs trotted uphill. Similarly, the activity of all five muscles was positively correlated with the amplitude of rearward-directed horizontal force. Furthermore, all except the superficial gluteus and adductor magnus muscles displayed significantly reduced activity when the dogs trotted downhill and negative correlations with the amplitude of forward-directed horizontal force. If a retractor moment was not present during level running, activity of the retractor muscles would not be expected to decrease relative to level running when the dogs ran

downhill or resisted forward-directed horizontal forces as they ran. Thus, these results are consistent with the hindlimb acting as a lever during constant speed running on level surfaces.

Significant increases in activity of the five primary retractor muscles were also observed when the dogs ran with additional mass attached to their hind feet. We anticipated increased activity in response to increased distal limb inertia during the end of swing phase, when the forward swing of the limb must be reversed by the retractor muscles. We did not, however, predict increased activity during stance phase as was observed in all five primary retractor muscles (Fig. 5B). This result suggests that in addition to producing retraction during swing phase of the ipsilateral limb, the retractor muscles also help to stabilize the pelvis against moments induced by protraction of the contralateral limb during the beginning of its swing phase. Specifically, we suspect that the weight of the contralateral limb during swing phase results in an adducting moment at the hip joint of the stance phase limb that tends to collapse the pelvis on the support limb. The primary retractor muscles also have a capacity to abduct the limb. Thus, activity of the primary retractor muscles during the beginning of stance phase may also stabilize the pelvis against an adducting moment induced by the contralateral limb during its swing phase.

Hindlimb retractors that cross the knee joint

When dogs trot at constant speed on level surfaces, the three hindlimb retractor muscles that cross the knee joint, the caudal part of the biceps femoris, the semitendinosus and the gracilis muscles, are primarily associated with initiating the swing phase. Presumably, they function to flex the knee joint at the beginning of swing phase. All three muscles became active at the end of stance phase and were most active during the first 20% of ipsilateral swing phase. Addition of mass to the hind foot resulted in substantial increases in the activity of these muscles during the beginning of swing phase, consistent with the function of initiating swing phase. None of these three 'hip retractor muscles' displayed more than a trace of activity that was associated with retraction of the hindlimb during trotting on the level treadmill.

Previous recordings indicate that the pattern of activity of the semitendinosus muscle in trotting cats (English and Weeks, 1987) and horses (Robert et al., 1999) is similar to that reported here for dogs. In rats, however, the semitendinosus muscle exhibits two pulses of activity, one at the beginning of swing phase, as in dogs, and another during the middle of support phase. Activity of the caudal part of the biceps femoris muscle in trotting cats (Rasmussen et al., 1978) and the gracilis muscles of trotting cats and rats (Nicolopoulos-Stourmaras and Iles, 1984) is reported to be approximately 180 deg. out of phase with the activity in dogs, occurring at the end of ipsilateral swing phase and the first half of support phase of cats or in the middle of support phase of rats.

When the dogs trotted uphill, the hip retractor function of these muscles became apparent. All three muscles exhibited a second pulse of activity during the end of ipsilateral swing phase and the beginning of stance phase during uphill trotting. Activity of these muscles was also positively correlated with the level of rearward-directed horizontal force. In contrast to the primary retractor muscles, these muscles did not decrease their activity relative to level trotting when the dogs ran downhill and activity level was not negatively correlated with amplitude of forward-directed horizontal force.

In summary, the hindlimb retractor muscles that cross the knee joint do not contribute to limb retraction during constant speed running on level surfaces in dogs. During constant speed, these

'hindlimb retractors' function primarily to initiate ipsilateral swing phase, presumably to flex the knee joint. They do, however, participate in limb retraction when dogs apply larger propulsive forces to the ground during uphill running and pulling forward against a rearward-directed resisting force.

Protractors of the hindlimb

Because of its inaccessibility, the psoas muscle was not analyzed in this study. The psoas muscle is recognized as an important protractor of the hindlimb. Thus, we ask readers to keep in mind that our discussion of the protractor muscles is limited by a lack of information from this muscle.

When dogs trot on level surfaces, both the tensor fasciae latae muscle and the two heads of the sartorius muscle function as protractors of the hindlimb during swing phase. The two heads of the sartorius muscle play little or no role in support phase during level running. The activity patterns of these muscles suggest that they contribute to different components of swing phase. The tensor fasciae latae muscle was active at the end of stance phase, presumably to decelerate the rearward swing of the limb and initiate protraction at the beginning of swing phase. By contrast, both heads of the sartorius muscle were active primarily during the first half of swing phase, with peak activity occurring during the first 15–20% of the swing phase. Activity of the tensor fasciae latae muscle at the end of stance phase may also be important in the production of the protractor moment at the hip that has been observed to occur during the second half of stance (Carrier et al., 1998). The tensor fasciae latae muscle of trotting horses (Robert et al., 1999) exhibits a pattern of activity that is similar to that reported here for trotting dogs. By contrast, the sartorius and tensor fasciae latae muscles of trotting cats are active throughout most of support phase and the first half of swing phase (Rasmussen et al., 1978). This suggests that these two biarticulate muscles play a greater role in knee extension during a running step in cats than in dogs.

Results from the force manipulations are also consistent with protraction of the hindlimb during swing phase as the primary function of these muscles during level running. Adding mass to the posterior trunk over the pelvic girdle increased the activity of all three of these muscles, but the increased activity was associated with early and mid swing phase rather than with stance phase. Running uphill also increased the activity of these muscles primarily during the first half of swing phase as would be expected from the increased work of lifting the limb. Also consistent with the function of hindlimb protraction during swing phase is the observation of decreased activity during late support phase in the case of the tensor fasciae latae and during the first half of swing phase in the case of the two heads of the sartorius muscle when the dogs ran downhill. In all three muscles, running downhill was also associated with elevated activity during stance phase, consistent with the production of a protracting moment on the hindlimb to provide braking in the forward direction. The final bit of evidence that is consistent with these three muscles functioning primarily as protractors during swing phase when dogs trot on level surfaces is the observation that adding mass to the hind foot produced elevated activity during the very end of stance phase and the first half of swing phase.

Comparison with other species

In all cases in which a comparison can be made between horses (Robert et al., 1999) and dogs, the two species appear to exhibit the same basic patterns in the activity of extrinsic appendicular muscles of the hindlimb. By contrast, activity of the extrinsic hindlimb muscles appears to be different in dogs from both cats and rats

(Rasmussen et al., 1978; Nicolopoulos-Stournaras and Iles, 1984). Most striking, the EMG recordings suggest that cats and in particular rats, differ from dogs and horses in relying on active retraction of the hindlimb during the second half of support phase. Both horses and dogs are recognized as being highly specialized for endurance running. Thus, it is tempting to speculate that cursorial specializations include changes in body configurations that reduce the reliance on active retraction of the hindlimb during running at constant speed.

Integration of hindlimb and hypaxial muscle function

Recruitment patterns of the oblique hypaxial muscles in trotting dogs have been attributed to the need to stabilize the trunk against torques in the sagittal plane imposed on the axial musculo-skeletal system by limb retraction and protraction moments (Fife et al., 2001). The activity patterns of hindlimb retractor and protractor muscles described here, as well as those reported for the forelimbs of trotting dogs (Carrier et al., 2008), are consistent with this hypothesis. During trotting on level surfaces, the primary retractor muscles of the hindlimb of dogs become active during the last 30% of ipsilateral swing phase and remain active during the first 30% of support phase. This activity period corresponds to the deceleration and reversal of the forward swing of the hindlimb during the end of swing phase and the production of a retractor torque by the hindlimb during the beginning of support phase (Carrier et al., 1998). During this same period, the abdominal internal oblique muscle is active (Fife et al., 2001). Thus, the activity periods of the primary retractor muscles of the hindlimb coincide more or less perfectly with the activity period of the abdominal internal oblique muscle.

A similar correspondence between the activity of the internal oblique muscle and the primary retractor muscles of the hindlimb occurs during trotting uphill and downhill. When dogs trot uphill, retractor muscles such as the cranial portion of the biceps femoris, the medial gluteus and the semimembranosus greatly increase the amplitude of their activity and remain active for much longer in the support phase. These increases in amplitude and period match the changes in the activity of the internal oblique muscle. By contrast, when dogs trot downhill, activity of the primary retractor muscles of the hindlimb is greatly reduced in both amplitude and duration and there is a coincident reduction in the activity of the internal oblique muscle.

These observations are consistent with the internal oblique muscle stabilizing the trunk against torques in the sagittal plane induced by hindlimb retraction (Fife et al., 2001). The architecture of the internal oblique muscle, with its origin on the ilium and its cranio-ventral fiber orientation, is ideally suited to stabilize the pelvis against the applied torque of the hindlimb retractor muscles during the end of swing phase and early hindlimb support when trotting on level surfaces and when dogs run uphill. Activity of the internal oblique muscle may also help support the trunk against the gravitational and inertial loads during deceleration in the vertical direction that causes the middle portion of the trunk to sag ventrally during the middle of support phase of a trotting step (Ritter et al., 2001).

The abdominal external oblique muscle becomes active later in the support phase of the hindlimb, at approximately 22% of support phase (Fife et al., 2001). This activity precedes the initiation of a protractor moment at the hip by approximately 50 ms (Carrier et al., 1998). During the second half of hindlimb support, activity of the abdominal external oblique muscle may, therefore, stabilize the

trunk against a hindlimb-induced torque that tends to retract the pelvis, allowing the hindlimb to extend without significant extension of the vertebral column.

When dogs trot uphill, and the hip protractor torque at the end of stance is presumably reduced (e.g. see response of the tensor fasciae latae muscle in Fig. 3A), activity of the abdominal external oblique muscle is greatly reduced relative to level running (Fife et al., 2001). A coincidence also occurs between the activity of the abdominal external oblique muscle and the activity of main protractor muscles of the hindlimb (tensor fasciae latae and sartorius muscles) when dogs trot downhill. Compared to running on a level surface, both the hindlimb protractor muscles and the abdominal external oblique exhibit dramatic increases in activity during downhill trotting. These observations are consistent with the external oblique muscle stabilizing the trunk against torques in the sagittal plane induced by hindlimb protractor muscles (Fife et al., 2001).

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