RESEARCH ARTICLE

Activity of extrinsic limb muscles in dogs at walk, trot and gallop

Stephen M. Deban[1,*], Nadja Schilling[2,3] and David R. Carrier[4]

[1]Department of Integrative Biology, 4202 East Fowler Avenue, SCA 110, University of South Florida, Tampa, FL 33620, USA,
[2]Institute of Systematic Zoology and Evolutionary Biology, Friedrich-Schiller-University, Erbertstrasse 1, 07743 Jena, Germany,
[3]Small Animal Clinic, University of Veterinary Medicine Hannover Foundation, Bünteweg 9, 30559 Hannover, Germany and
[4]Department of Biology, 201 South Biology Building, University of Utah, Salt Lake City, UT 84112, USA

*Author for correspondence (sdeban@usf.edu)

SUMMARY

The extrinsic limb muscles perform locomotor work and must adapt their activity to changes in gait and locomotor speed, which can alter the work performed by, and forces transmitted across, the proximal fulcra of the limbs where these muscles operate. We recorded electromyographic activity of 23 extrinsic forelimb and hindlimb muscles and one trunk muscle in dogs while they walked, trotted and galloped on a level treadmill. Muscle activity indicates that the basic functions of the extrinsic limb muscles – protraction, retraction and trunk support – are conserved among gaits. The forelimb retains its strut-like behavior in all gaits, as indicated by both the relative inactivity of the retractor muscles (e.g. the pectoralis profundus and the latissimus dorsi) during stance and the protractor muscles (e.g. the pectoralis superficialis and the omotransversarius) in the first half of stance. The hindlimb functions as a propulsive lever in all gaits, as revealed by the similar timing of activity of retractors (e.g. the biceps femoris and the gluteus medius) during stance. Excitation increased in many hindlimb muscles in the order walk–trot–gallop, consistent with greater propulsive impulses in faster gaits. Many forelimb muscles, in contrast, showed the greatest excitation at trot, in accord with a shorter limb oscillation period, greater locomotor work performed by the forelimb and presumably greater absorption of collisional energy.

Key words: electromyography, EMG, *Canis*, locomotion, symmetrical gait, asymmetrical gait.

INTRODUCTION

The extrinsic limb muscles are crucial functional components for locomotion in quadrupedal mammals. These muscles span the proximal fulcra of the limbs and perform work of propulsion and braking (Gray, 1968; Gregersen et al., 1998). Forces that are required to counteract inertia and gravity are transmitted by the extrinsic muscles between the limbs and the trunk. With changes in gait and locomotor speed, these muscles must produce or accommodate changes in the work performed and the forces transmitted, thus their activity must be modulated in its timing and/or intensity. This study examined the changes in the activity of the extrinsic limb muscles of dogs as they walked, trotted and galloped.

The locomotor gaits employed by quadrupedal mammals differ in a variety of ways including the speeds at which they are employed, footfall patterns, limb and trunk kinematics, and center of mass dynamics (e.g. Muybridge, 1899; Howell, 1944; Gray, 1944; Gray, 1968; Hildebrand, 1966; Gambaryan, 1974; Hildebrand, 1977; Cavagna et al., 1977; Ruina et al., 2005; Bertram and Gutmann, 2009). These differences are likely to influence the function of the extrinsic limb muscles. The transition from trot to gallop, for example, can dramatically alter the magnitude and timing of the locomotor forces that a given limb experiences. A forelimb that shares its stance phase with the contralateral hindlimb in the trot can also share the gravitational and inertial forces, whereas the same forelimb may be the only limb on the ground in the gallop and must handle these forces alone. The limbs may accommodate these and other changes in locomotor forces by altering the activity of the extrinsic limb muscles.

In addition to adapting to gait changes, muscles in the forelimb and hindlimb that have comparable basic functions (e.g. limb retraction) may differ in their activity even within a single gait. Differences are expected because during level, steady-speed locomotion, the hindlimb is primarily propulsive while the forelimb engages more in braking [e.g. in dogs (Budsberg et al., 1987; Rumph et al., 1994; Bryant et al., 1987)], and because the forelimb has been shown to act more like a compliant strut during trotting than the hindlimb, which acts more like a lever (Gray, 1968; Carrier et al., 2008; Schilling et al., 2009; Lee, 2011). If these mechanical forelimb–hindlimb differences are consistently present in different gaits, corresponding differences in the activity of extrinsic muscles would be expected in all gaits.

In addition to differences in their mechanics, the forelimbs and hindlimbs differ in their anatomy and thus in how forces are transmitted between the trunk and the distal limb. The forelimb of mammals has a reduced skeletal connection to the trunk and forces are transmitted mainly *via* a unique muscular sling (Davis, 1949; Gray, 1968). This sling is particularly important in cursorial mammals such as dogs, which have a reduced or absent clavicle and thus lack any skeletal connection between the forelimb and the thorax (e.g. Howell, 1937; Hildebrand, 1962). Muscle excitation in the muscular sling of the forelimb may therefore be expected to reflect braking forces that pass through the proximal fulcrum as well as the absorption of collisional energy (Ruina et al., 2005; Bertram and Gutmann, 2009). This situation is different from that of the hindlimb, in which forces aligned with the limb axis can pass through the hip joint [e.g. in dogs (Page et al., 1993; Shahar and Banks-Sills, 2002)].

Despite all these differences, some basic locomotor parameters are conserved among gaits. Therefore, it is reasonable to expect that the extrinsic muscles retain their basic functions, for example limb retraction, limb protraction, or support of the trunk against gravity and inertial forces. The angular excursions of limbs are conserved across gaits [e.g. in dogs (Goslow et al., 1981; Fischer and Lilje, 2011)]; therefore, the timing of activity of the extrinsic limb muscles relative to touch-down and lift-off events may be conserved. However, increases in locomotor speed are expected to be coupled with increases in muscle excitation in all of the extrinsic muscles, because with increasing speed the mechanical cost of transport increases (Cavagna et al., 1977; Willems et al., 1995) and the force impulse of a given footfall increases [e.g. in dogs (Budsberg et al., 1987; Rumph et al., 1994; Bertram et al., 2000; Bockstahler et al., 2007; Walter and Carrier, 2007; Mölsa et al., 2010; Voss et al., 2010)].

We examined the activity of 23 extrinsic muscles of the forelimbs and hindlimbs in dogs as they walked, trotted and galloped on the treadmill to evaluate whether: (1) the timing of activity indicates that the basic functions of the muscles – as a protractor, retractor, fulcrum stabilizer or muscular sling – are conserved across gaits; (2) the forelimb and hindlimb retain their functions as a strut and a propulsive lever at the proximal fulcrum, respectively, in all gaits; and (3) the level of muscle excitation in both the forelimb and hindlimb muscles increases with increasing locomotor speed (i.e. walk<trot<gallop). In addition to recording the activity of extrinsic limb muscles, we examined the effects of gait on the activity of a trunk muscle, the thoracic external oblique muscle, which has been shown to play a role in stabilizing the trunk against torques produced by the extrinsic limb muscles (Fife et al., 2001).

MATERIALS AND METHODS

Twelve mixed-breed dogs (*Canis lupus familiaris* Linnaeus 1758) of 25±1 kg (mean ± s.e.m.) body mass were used as subjects to record the electromyographic (EMG) activity of 23 muscles of the forelimb and hindlimb as well as one trunk muscle. The dogs walked, trotted and galloped on a horizontal motorized treadmill. Treadmill speed was 1.32±0.04 m s^{-1} (mean ± s.e.m.) during walking, 2.43±0.04 m s^{-1} during trotting and 4.43±0.12 m s^{-1} during galloping. All dogs displayed a lateral sequence walk, a trot with synchronized diagonal limb movements (Hildebrand, 1966) and a transverse gallop (Hildebrand, 1977) with a forelimb-initiated aerial phase (Bertram and Gutmann, 2009). EMG signals were recorded from eight dogs walking, 12 dogs trotting and nine dogs galloping with the ipsilateral limb acting as either the trailing limb (i.e. the first limb to touch down) or the leading limb (i.e. the second limb to touch down). Five dogs switched trailing and leading limbs and provided EMG recordings for both leads while galloping.

The experimental protocol and subjects used in this study are the same as those used in previous studies (Carrier et al., 2006; Carrier et al., 2008; Schilling and Carrier, 2009; Schilling et al., 2009; Schilling and Carrier, 2010). Dogs were obtained from local animal shelters in Utah (USA) and trained to locomote unrestrained on the treadmill. EMG recordings began on the third or fourth day following surgical implantation of electrodes and continued for 5–6 days. Electrodes were removed no later than 11 days after implantation. All dogs were adopted as pets after a period of recovery. All procedures conformed to the guidelines of the University of Utah Institutional Animal Care and Use Committee.

Electrode implantation and EMG recording

Surgical implantation of the electrodes, recording of the muscle activity and data analysis were conducted as described previously (Carrier et al., 2006; Carrier et al., 2008; Schilling et al., 2009). Sew-through electrodes (Basmajian and Stecko, 1962) were implanted at 27 muscle sites unilaterally (Fig. 1). The forelimb muscles examined were: protractors of the proximal forelimb, the m. omotransversarius, m. cleidobrachialis, m. pectoralis superficialis transversus (which also functions in retraction) and m. pectoralis superficialis descendens; retractors of the forelimb, the posterior portion of the m. pectoralis profundus and the ventral portion of the m. latissimus dorsi; stabilizers of the fulcrum of the forelimb on the trunk, the m. serratus ventralis cervicis inserting on the transverse processes of C6, the m. rhomboideus thoracis medial to the dorsal margin of the scapula, and the cervical and thoracic parts of the m. trapezius; and a muscle that supports the trunk against gravity and vertical loading, the m. serratus ventralis thoracis, inserting on ribs 5 and 6 (Fig. 1A–C). The hindlimb muscles examined were: femoral protractors, the m. tensor fasciae latae, m. rectus femoris, and the cranial and caudal parts of the m. sartorius; femoral retractors, the cranial part of the m. biceps femoris, m. gluteus superficialis, m. gluteus medius, m. adductor magnus and the caudal belly of the m. semimembranosus; and muscles that both retract the femur and flex the knee joint, the m. semitendinosus, m. gracilis and the caudal part of the m. biceps femoris (Fig. 1D–F). The thoracic portion of the m. external oblique, a trunk muscle with a dorsocaudal fiber orientation, was also examined using patch electrodes implanted at the fourth and fifth intercostal spaces (Fig. 1A,B) (Deban and Carrier, 2002). The anatomy of these muscles is described in Evans (Evans, 1993) and is illustrated in Fig. 1.

EMG signals were amplified approximately 2000 times, digitally sampled at 4000 Hz, and filtered above 1000 Hz and below 100 Hz. Dogs were simultaneously imaged in lateral view at 60 Hz to correlate locomotor events, such as footfalls, with the timing of muscle activity. Images were synchronized with EMG signals as previously described (Carrier et al., 2008). Additionally, a signal of vertical acceleration throughout the locomotor cycle was sampled from an accelerometer mounted to the dog's back.

Analysis of EMG signals
Stride normalization

To examine the relationship between muscle excitation and locomotor events and to facilitate comparisons among subjects and trials, time-normalized stride average electromyograms (EMGs) were generated for each muscle site from 20 strides from each dog (for details, see Carrier et al., 2008). The stride averages were generated from rectified EMGs using a sampling window that was identified with the accelerometer signal. The sampling window began and ended with the initiation of limb support ipsilateral to the instrumented side. The image sequences were used to identify the point in the accelerometer signal that corresponded to the touch-down of the forelimb or hindlimb ipsilateral to electrode implantation. The sampling window varied slightly in duration during a trial and, consequently, differed in the number of recorded data points. To enable averaging across multiple strides of different durations, each EMG sample was time-normalized using a purpose-written LabVIEW program (National Instruments, Austin, TX, USA) to generate a new sample consisting of 120 bins in which all the point values from the original EMG sample were partitioned. This stride normalization was accomplished by placing the sum of the point values from the original sample that occurred in the first 120th of the stride into the first of the 120 bins. 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

ad   m. adductor magnus
cd   m. cleidobrachialis
bd   m. biceps femoris caudal
br   m. biceps femoris cranial
gm   m. gluteus medius
gr   m. gracilis
gs   m. gluteus superficialis
ld   m. latissimus dorsi
oe   m. obliquus externus
om   m. omotransversarius
pd   m. pectoralis superficialis desc.
pp   m. pectoralis profundus
pt   m. pectoralis superficialis trans.
rf   m. rectus femoris
rh   m. rhomboideus
sc   m. serratus ventralis cervicis
sd   m. sartorius caudal
st   m. semitendinosus
sm   m. semimembranosus
sr   m. sartorius cranial
sv   m. serratus ventralis thoracis
tc   m. trapezius pars cervicalis
tt   m. trapezius pars thoracica
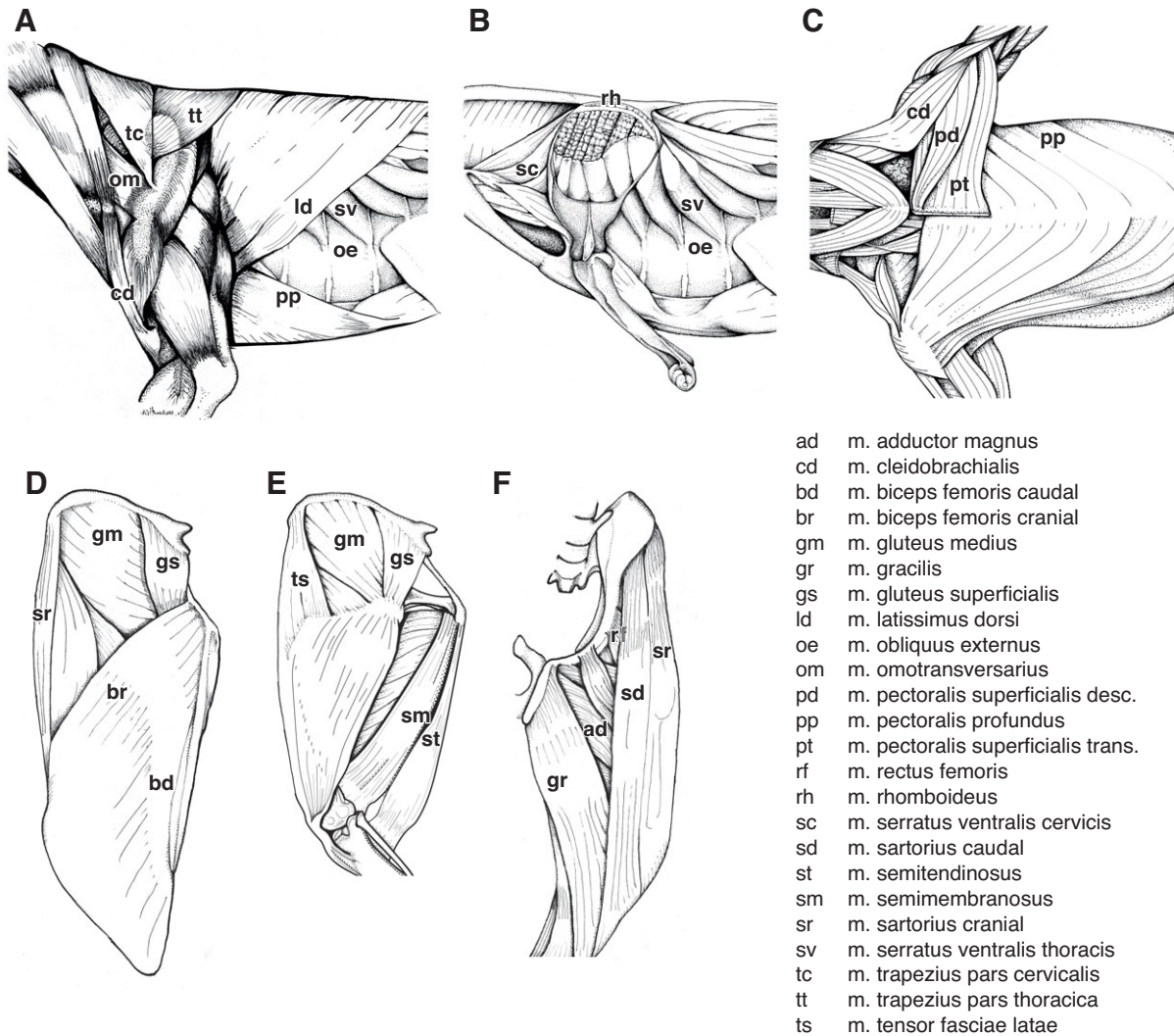ts   m. tensor fasciae latae

Fig. 1. Illustrations of the extrinsic limb muscles of the canid pectoral (A–C) and pelvic (D–F) girdles with muscle abbreviations indicating the electrode placement used in this study (modified from Carrier et al., 2006; Carrier et al., 2008; Schilling et al., 2009). Forelimb: lateral view of the superficial muscles with the m. cutaneus trunci removed (A), deep appendicular muscles in lateral view (B) and ventral view of the superficial muscles (C). Hindlimb: lateral view of the superficial muscles (D), lateral view with the m. biceps femoris removed (E) and medial view of the superficial muscles (F).

(i.e. strides) for a given muscle or muscle site. The resulting stride average for each site thus contained a series of 120 bins that represented the average activity of that muscle site during the locomotor cycle. The averaging process also allowed comparison of gaits with different stride durations (Figs 2, 3).

Amplitude normalization

The effects of gait on the EMG patterns were illustrated by amplitude-normalizing the EMG averages against the average EMG amplitude during the trot. This normalization was performed in two steps. First, the average value for the 120 bins of the trot was calculated, and each bin of the walk, trot and gallop trials was divided by this average value; this was performed for each dog separately. Second, summary statistics for each gait were calculated across all dogs, including mean, median, standard error, and upper and lower quartiles. By normalizing the values for each dog to mean trot activity prior to generating statistics for all dogs, the pattern from one dog did not overwhelm the pattern from another (because of differences in EMG signal strength due to electrode properties, for

example). The resulting EMG patterns across all dogs for a given gait were graphed as median values and lower and upper quartiles (Figs 4, 5).

Phase normalization

EMG patterns were depicted with stance and swing phases normalized separately to the same length for all gaits to facilitate comparisons of the timing of muscle activity with reference to footfall events (Figs 4, 5). The 120-bin stride averages of each gait for each dog were divided into stance and swing phases, and the stance-phase EMG signals were interpolated with a cubic spline and then downsampled to yield 60 bins (original lengths of the stance phases were 71 bins for walk, 45 for trot and 33 for gallop). The value of each bin was then divided by the average of all bins of the trot to normalize voltages and remove electrode differences (as above). The same was conducted for swing-phase EMG signals. Stance and swing signals were recombined to yield a 120-bin EMG average comprising 60 bins of stance and 60 bins of swing phase activity.
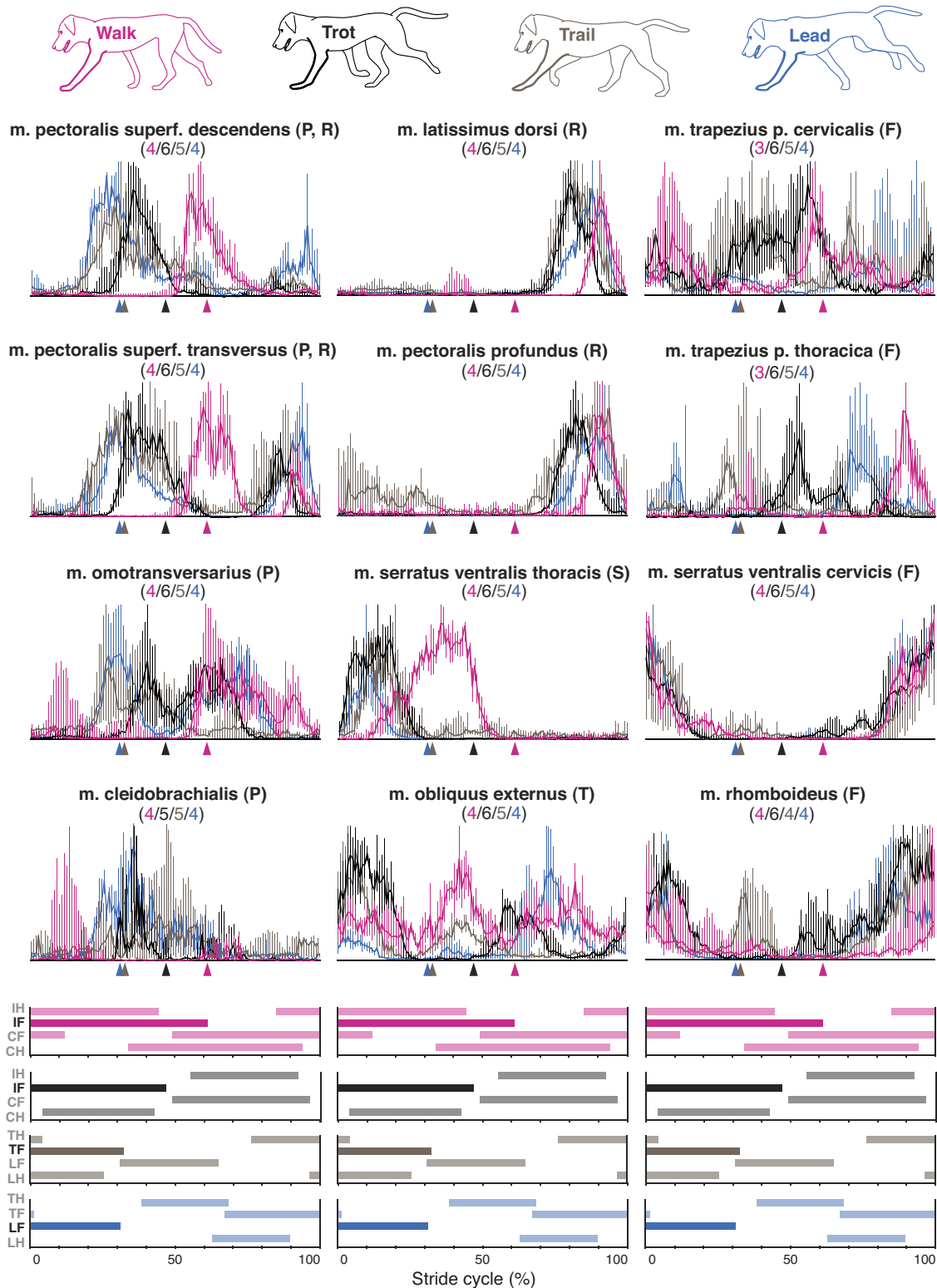
Fig. 2. Activity patterns of extrinsic forelimb muscles and a trunk muscle shown as stride-normalized electromyographs (EMGs) (median plus upper and lower quartiles for each of 120 bins) averaged across dogs and 20 strides from each gait (colors throughout are keyed by dog outlines). Each plot is scaled to the maximum amplitude observed at a given recording site, hence EMG amplitudes are not comparable among plots and among gaits within a given plot. The stride cycle (horizontal axis for all plots) starts with the touch-down of the forelimb ipsilateral to the electrodes, which functions during galloping as either the trailing or the leading forelimb. The footfall pattern at the bottom shows stance phases (solid bars) of the ipsilateral hindlimb (IH), ipsilateral forelimb (IF), contralateral forelimb (CF), contralateral hindlimb (CH), and likewise the leading (LF, LH) and trailing (TF, TH) limbs. Colored triangles indicate the lift-off of the ipsilateral forelimb during each gait. Letters in parentheses after muscle names indicate their hypothesized function as a protractor (P), retractor (R), fulcrum stabilizer (F), muscular sling (S) or knee flexor (K) as well as in trunk stabilization (T). Numbers in parentheses indicate sample sizes for the respective gaits.
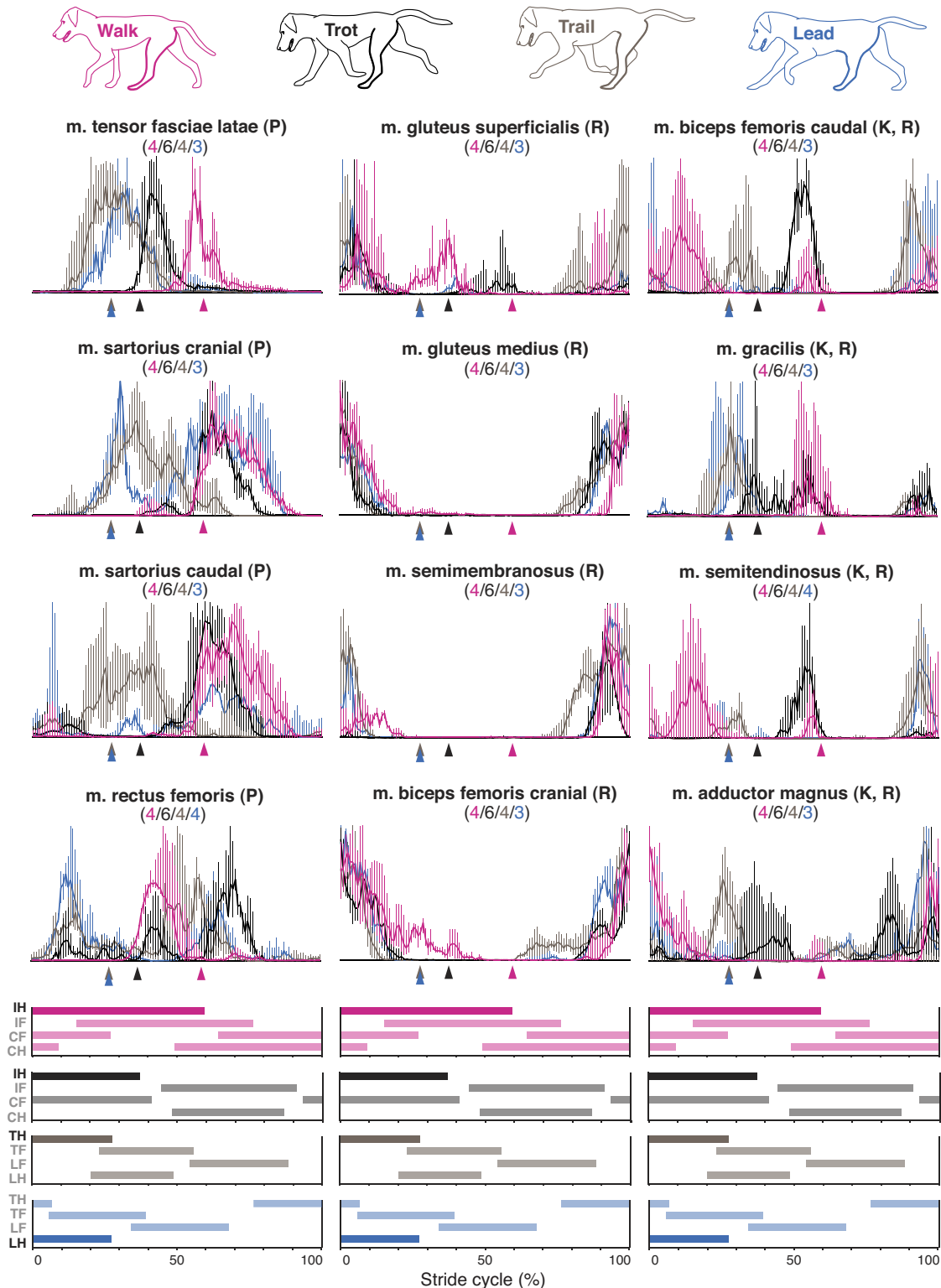
Fig. 3. Activity patterns of extrinsic hindlimb muscles shown as stride-normalized EMGs averaged across dogs and 20 strides from each gait. The stride cycle (horizontal axis for all plots) starts with the touch-down of the hindlimb ipsilateral to the electrodes, which functions during galloping as either the trailing or the leading hindlimb. Indications as in Fig. 2.

Analysis of muscle excitation per stride

The level of muscle excitation occurring during a stride was expected to increase when dogs switched from a walk to a trot and to increase further when they transitioned from a trot to a gallop, because of the increase in the distance covered per stride and the greater peak forces. To test these predictions, changes in both integrated EMG area (i.e. the sum of the bins of the stride- and amplitude-normalized EMG signal for each dog) and the root mean
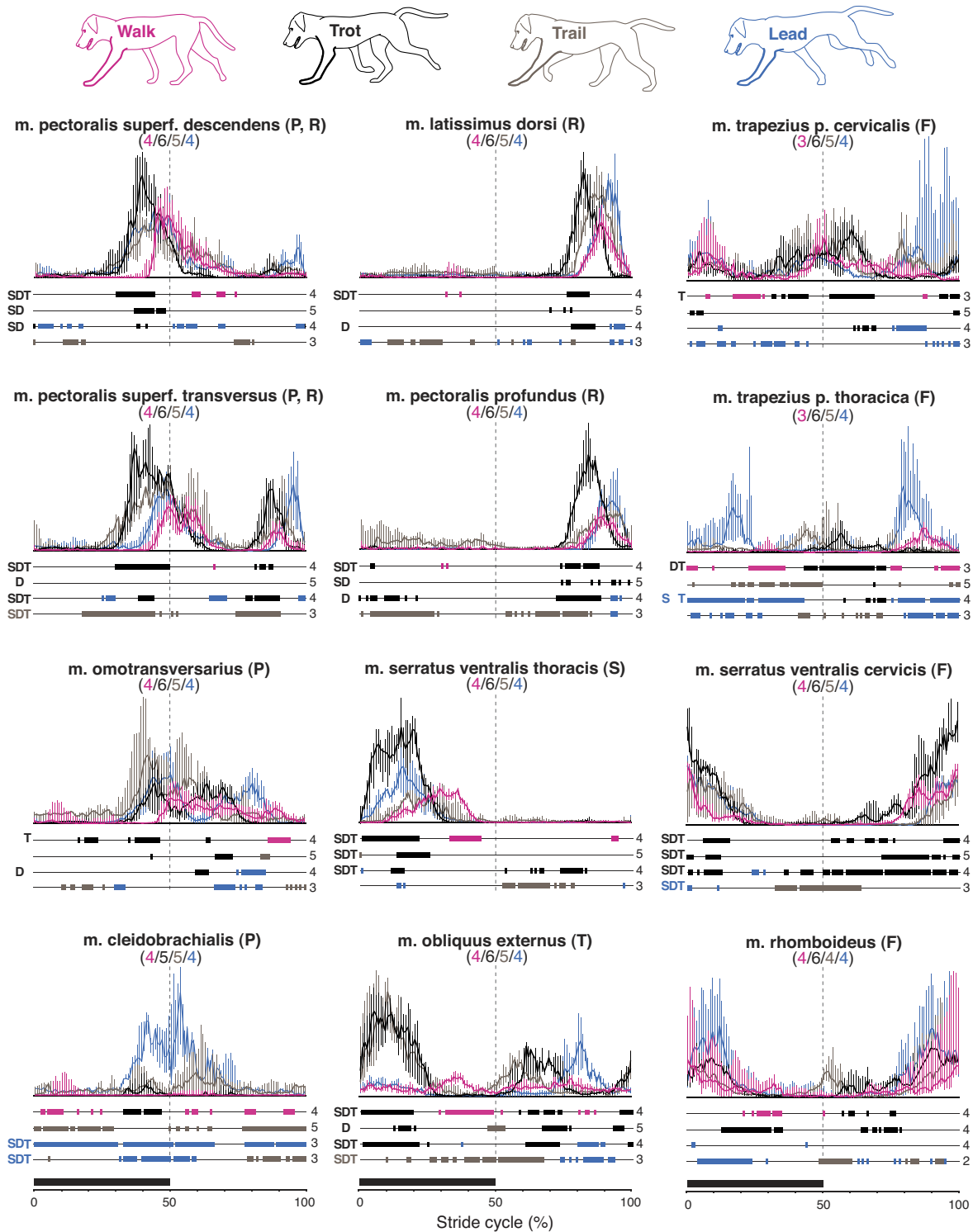
Fig. 4. Activity patterns of extrinsic forelimb muscles and a trunk muscle shown as phase-normalized EMGs averaged across dogs and 20 strides from each gait. Stance phase (black bar) and swing phase of the forelimb ipsilateral to the electrodes are normalized to 50% of the cycle in all gaits. Each plot has a single y-axis, hence EMG amplitudes may be compared among gaits within a given plot. Colored blocks below EMG traces indicate bin-by-bin differences in amplitude between gaits, with the color indicating the gait with significantly greater amplitude; no block indicates no difference. Letters to the left of the block indicate by color which gait has significantly higher root mean square (r.m.s.) excitation as calculated on a per-stride (S), per-distance (D) or per-time (T) basis. Numbers to the right of the blocks indicate the number of dogs in each comparison. Other indications as in Fig. 2.

square (r.m.s.; the square root of the mean of the squares of the bins of the stride- and amplitude-normalized EMG signal) were examined for each muscle or muscle site recorded, as follows. The integrated

EMG area (hereafter, 'EMG area') during walking was subtracted from the area during trotting. The r.m.s. during walking was similarly subtracted from the r.m.s. during trotting. These differences
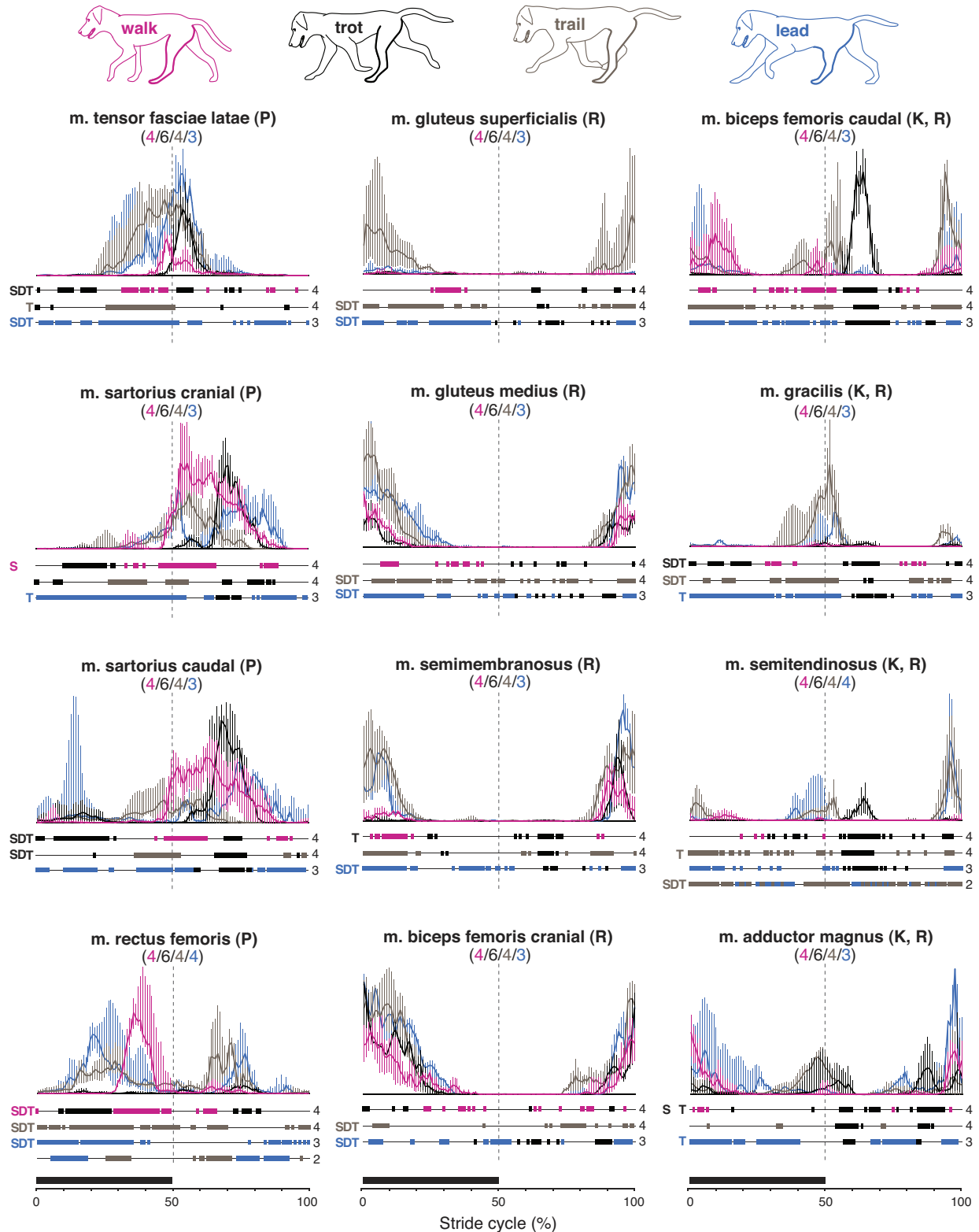
Fig. 5. Activity patterns of extrinsic hindlimb muscles shown as phase-normalized EMGs averaged across dogs and 20 strides from each gait. Stance phase (black bar) and swing phase of the hindlimb ipsilateral to the electrodes are normalized to 50% of the cycle in all gaits. Each plot has a single *y*-axis, hence EMG amplitudes may be compared among gaits within a given plot. Other indications as in Figs 2 and 4.

were computed for every muscle separately for each dog. Likewise, the EMG area and the r.m.s. of the trotting signals were subtracted from those of the galloping signal (leading and trailing limbs). An

increase in excitation as the dogs moved from a walk to a trot or from a trot to a gallop would yield positive values for this difference, whereas no increase in excitation would yield a value of zero (i.e.

Table 1. Differences in muscle recruitment among gaits, shown as differences in integrated area (upper) and r.m.s. (lower) between pairs of gaits

Muscle	Trot–Walk				Trail–Trot				Lead–Trot				Lead–Trail			
	N	Stride	Distance	Time	N	Stride	Distance	Time	N	Stride	Distance	Time	N	Stride	Distance	Time
m. pectoralis superf. descendens	4	32.00	69.79	128.62*	5	11.54	−54.07	64.39	4	−1.89	−59.15*	30.49	3	−12.09	−11.88	−25.19
	4	0.65*	1.45*	2.41*	5	−0.38*	−1.71*	−0.37	4	−0.52*	−1.66*	−0.64	3	−0.09	−0.04	−0.15
m. pectoralis superf. transversus	4	79.98*	157.82*	201.23*	5	19.24	−45.72*	85.68	4	−18.61*	−85.20*	−12.58	3	−50.28*	−62.87*	−120.40
	4	1.06*	2.12*	2.78*	5	−0.02	−1.09*	0.48	4	−0.52*	−1.58*	−0.74*	3	−0.60*	−0.71*	−1.41
m. omotransversarius	4	20.43	50.04	111.49*	5	97.83	61.67	281.63	4	38.70	−23.14	110.77	3	−6.36	−4.28	−8.64
	4	0.08	0.31	1.19*	5	1.20	0.64	3.47	4	0.01	−1.02*	0.41	3	−0.46	−0.49	−0.98
m. cleidobrachialis	4	−94.56	−140.37	−51.71	5	969.51	1266.71	2415.54*	3	1303.10*	1564.29*	3215.81*	3	805.54*	1105.93*	2077.49
	4	−1.94	−2.79	−0.84	5	11.42	14.64	29.18	3	16.96*	19.30*	41.41*	3	11.77*	14.95*	28.71
m. latissimus dorsi	4	70.61*	141.83*	187.33*	5	40.74	−8.90	144.46*	4	1.29	−55.77	41.88	3	−13.20	−12.68	−22.64
	4	1.42*	2.86*	3.89*	5	0.11	−1.18	1.12	4	−0.31	−1.57*	0.01	3	−0.14	−0.14	−0.22
m. pectoralis profundus	4	81.05*	158.07*	202.09*	5	−4.05	−73.75*	29.71	4	−41.64*	−113.03*	−66.43	3	−34.08*	−41.12*	−80.08
	4	1.63*	3.22*	4.02*	5	−0.68*	−2.24*	−0.96	4	−0.71	−1.96*	−1.03	3	−0.09	−0.07	−0.19
m. serratus ventralis thoracis	4	63.55*	128.97*	176.69*	5	−69.79*	−166.25*	−136.94*	4	−75.63*	−158.98*	−147.09*	3	−4.61	−3.31	−8.67
	4	1.53*	3.05*	3.89*	5	−1.43*	−3.29*	−2.87*	4	−1.29*	−2.79*	−2.47*	3	0.01	0.06	0.07
m. obliquus externus	4	73.53*	145.29*	191.10*	5	−18.48	−93.47*	−6.63	4	−63.12*	−146.39*	−122.88*	3	−28.63*	−37.26*	−68.73
	4	1.14*	2.26*	2.80*	5	−0.28	−1.30*	−0.16	4	−0.75*	−1.77*	−1.40*	3	−0.37*	−0.48*	−0.88
m. trapezius p. cervicalis	3	25.52	67.35*	121.21*	5	82.26	63.45	258.28	4	85.78	74.95	246.73	3	41.69	62.49*	106.90
	3	0.26	0.77	1.43*	5	0.87	0.55	2.80	4	1.38	1.41	3.85	3	0.86	1.28	2.13
m. trapezius p. thoracica	3	32.72*	74.69	128.95*	5	119.88	91.78	321.47	4	611.91*	841.88	1531.24*	3	418.23	629.32	1046.60
	3	0.49	1.26*	2.19*	5	1.40	0.75	3.85	4	8.24*	11.24	20.75*	3	5.75	8.73	14.43
m. serratus ventralis cervicis	4	71.41*	143.31*	188.68*	5	−68.60*	−163.00*	−131.24*	4	−64.55*	−146.21*	−123.26*	3	11.17	13.47	25.11
	4	1.07*	2.18*	2.84*	5	−1.04*	−2.46*	−2.01*	4	−0.73*	−1.74*	−1.31*	3	0.22*	0.30*	0.53
m. rhomboideus	4	−50.17	−81.17	1.95	4	28.81	−24.87	106.52	4	95.41	94.33	288.59	2	37.11	57.84	93.81
	4	−0.75	−1.25	−0.20	4	0.56	0.05	1.78	4	1.18	1.15	3.55	2	0.47	0.73	1.18
m. tensor fasciae latae	4	64.53*	91.71*	142.5*	4	166.84*	186.46*	456.39*	3	199.31*	258.64*	563.17*	1	12.69	16.76	31.19
	4	1.93*	2.73*	4.11*	4	1.88	1.84	5.91*	3	2.41*	3.15*	7.78*	1	0.53	0.70	1.30
m. sartorius cranial	4	−71.50*	−79.94	−41.7	4	22.15	−1.40	106.81	3	53.50*	72.26*	211.29*	1	84.07	110.99	206.55
	4	−0.76*	−0.77	0.02	4	−0.18	−0.68	0.60	3	0.02	0.04	1.53*	1	0.99	1.31	2.44
m. sartorius caudal	4	29.00	48.49	97.6*	4	−57.16*	−95.71*	−77.83*	3	13.83	19.94	113.86*	1	43.25	57.11	106.27
	4	0.78*	1.19*	2.11*	4	−1.16*	−1.86*	−1.72*	3	−0.18	−0.20	0.94	1	0.44	0.59	1.09
m. rectus femoris	4	−807.83*	−993.80*	−976.9*	4	761.33*	945.46*	1883.53*	4	952.16*	1246.40*	2386.56*	2	−15.32	3.19	−29.43
	4	−16.86*	−20.76*	−20.52*	4	10.39*	12.91*	26.00*	4	14.76*	19.31*	36.95*	2	−2.07	−2.10	−4.87
m. gluteus superficialis	4	−34.38	−34.50	4.3	4	2448.44*	3053.74*	5830.87*	3	71.61*	94.38*	253.90*	1	−148.91	−196.60	−365.87
	4	0.32	0.65	1.75	4	38.31*	48.27*	91.85*	3	1.10*	1.41*	4.65*	1	−1.71	−2.26	−4.20
m. gluteus medius	4	−19.51	−14.29	28.5	4	211.79*	269.80*	578.31*	3	164.60*	211.45*	476.35*	1	−137.88	−182.04	−338.77
	4	−0.10	0.10	0.97	4	3.44*	4.29*	9.51*	3	3.02*	3.93*	8.68*	1	−2.01	−2.65	−4.94
m. semimembranosus	4	20.97	38.89	87.3*	4	262.34*	345.53	709.00*	3	160.44*	210.07*	470.51*	1	−240.15	−317.06	−590.05
	4	0.95	1.38	2.65*	4	3.43	4.40	9.81	3	2.56*	3.44*	8.38*	1	−2.91	−3.85	−7.16
m. biceps femoris cranial	4	−0.63	8.11	53.9	4	57.21*	55.52*	198.46*	3	31.35*	42.00*	155.76*	1	−14.92	−19.70	−36.66
	4	0.39	0.67	1.48	4	0.86*	0.80*	3.09*	3	0.58*	0.78*	2.66*	1	0.01	0.01	0.02
m. biceps femoris caudal	4	1.42	12.33	58.5	4	60.06	73.31	212.55	3	−14.23	−15.73	46.44	1	−124.61	−164.52	−306.17
	4	0.75	1.17	2.25	4	0.49	0.45	2.80	3	−0.58	−0.66	0.30	1	−2.36	−3.12	−5.80
m. gracilis	4	80.53*	111.02*	161.2*	4	752.15*	968.42*	1873.55*	3	336.15	437.93*	898.31*	1	−839.31	−1108.11	−2062.19
	4	1.66*	2.32*	3.49*	4	15.32*	19.85*	38.28*	3	6.16	8.00	16.84*	1	−15.31	−20.22	−37.62
m. semitendinosus	4	40.47	59.40	109.9	4	389.10*	559.49	1036.00*	4	330.82	461.35	893.85	2	−515.65*	−758.45*	−1294.20
	4	1.09	1.56	2.63	4	7.01	10.13	19.18*	4	7.16	10.03	19.71	2	−8.45*	−12.29*	−21.15
m. adductor magnus	4	30.88	49.44	98.9	4	−15.82	−42.25	21.34	3	81.50*	104.15*	274.64*	1	59.34	78.35	145.80
	4	0.45*	0.69	1.56*	4	−0.14	−0.49	0.63	3	0.96	1.27	3.83*	1	0.13	0.17	0.31

Differences were calculated for the entire stride (Stride), per unit distance (Distance) and per unit time (Time). *N* is the number of dogs used in each comparison. Asterisks indicate significant differences between gaits. See Materials and methods for details of statistical tests.

the null hypothesis) and a decrease would yield negative values (Table 1). Differences were compared with the hypothesized difference of zero by computing 97.5th and 2.5th percentiles of the difference when averaged across dogs. If these percentiles encompassed zero, the null hypothesis was accepted; if the percentiles failed to encompass zero (i.e. both 97.5th and 2.5th percentiles were greater than or less than zero), the null hypothesis was rejected and the change in muscle excitation across gaits was significant. A similar analysis was conducted to test whether muscle excitation differed between galloping gaits with a limb functioning as the leading or the trailing limb, by generating differences between leading-limb and trailing-limb excitation for each dog.

Analysis of muscle excitation per distance

Muscle excitation per unit distance traveled (i.e. per meter) was hypothesized to remain unchanged when dogs switched gaits, based on the premises that the metabolic work required to cover a given distance is independent of speed, and that muscle excitation is proportional to metabolic work. This was tested as above using differences in EMG area and r.m.s., but, prior to calculating the differences, the EMG area and r.m.s. values for each dog were divided by the average length (m) of 20 strides of the relevant gait for that dog.

Analysis of muscle excitation per time

The level of muscle excitation per unit time (i.e. per second) was also expected to increase as the dogs switched from a walk to a trot, and further increase as they transitioned to a gallop, due in part to the increase in forward speed. This was tested as above using differences in EMG area and r.m.s. (i.e. trot minus walk, gallop minus trot and leading limb minus trailing limb); however, prior to computing the differences, the EMG area and r.m.s. values for a given dog were divided by the average duration (s) of 20 strides for that dog.

Analysis of instantaneous muscle excitation during stance and swing

In addition to the expected changes in muscle excitation during the entire stride cycle as dogs switched gaits, changes in moment-to-moment excitation were expected. Muscles that function in hindlimb retraction, for example, were expected to show higher excitation during the stance phase in galloping *versus* trotting, reflected as higher EMG voltages. These expectations were tested by comparing, bin-by-bin, EMG voltages of the stride-, amplitude- and phase-normalized activities across gaits, as follows. Phase-normalized EMG averages (Figs 4, 5) were used to calculate, bin-by-bin, the differences between gaits (i.e. trot minus walk, leading limb at gallop minus trot, trailing limb minus trot and leading limb minus trailing limb). As described above, significant differences in instantaneous excitation between gaits for a given bin were indicated if the 2.5th and 97.5th percentiles of the difference for that bin failed to encompass zero, the value predicted by the null hypothesis of no change in activity.

RESULTS
Forelimb muscle timing

Muscles that are anatomically positioned to act as forelimb protractors – the cleidobrachialis, pectoralis superficialis descendens and omotransversarius – were active in the final third of stance and remained active into swing in all gaits (Figs 2, 4). Muscles that are positioned to act as forelimb retractors – the latissimus dorsi and pectoralis profundus – were active in the second half of the swing phase in all gaits. The exception to this pattern among the retractors is the m. pectoralis profundus in the trailing limb during galloping; it was active during stance. The m. pectoralis superficialis descendens and particularly the m. transversus showed a second, smaller burst of activity at the end of the swing phase in all gaits. In summary, with only minor variations in timing, the forelimb protractor and retractor muscles largely retained their functions in all gaits.

The m. serratus ventralis thoracis was active only during stance in all gaits, with activity extending from the time of touch-down to approximately two-thirds into the stance phase in trotting and galloping, and extending nearly the entirety of stance in walking. The cervical portion of the m. trapezius was active in two bursts in all gaits, centered around lift-off and touch-down of the ipsilateral

limb. In galloping, it additionally showed a burst of activity in the middle of the swing phase. The rhomboideus and serratus ventralis cervicis muscles showed a single large burst of activity that extended from mid swing to mid stance in all gaits.

Although the majority of forelimb muscles showed activity that was conserved in its timing across gaits, the m. trapezius p. thoracica showed patterns of activity that differed among gaits (Fig. 4). It was active in the second half of swing during walking, similar to the activation pattern of the major limb retractors. It was active in trot at the end of stance and throughout swing. In galloping, the muscle showed two bursts of activity in the leading limb; one burst occurred around midstance and the other during the second half of swing. In the trailing limb, the thoracic trapezius was active throughout stance.

The m. obliquus externus showed activity throughout the step cycle in walking, with the greatest activity in the second half of stance of the ipsilateral forelimb. (This muscle is included among the forelimb muscles because of the anterior electrode placement.) In trotting, this muscle showed two bursts of activity. The resulting bilateral activity may counteract sagging of the trunk. In galloping, the m. obliquus externus showed biphasic activity on the same side of the trailing limb as in trotting; however, on the side of the leading limb the larger burst during stance was much reduced, occurring when no other limbs were on the ground (Fig. 4).

Forelimb muscle excitation – walk *versus* trot

Seven of the 11 extrinsic forelimb muscles studied had significantly higher per-stride excitation in trotting than in walking (97.5th and 2.5th percentiles of the difference in EMG area or r.m.s. failed to encompass zero) – pectoralis superficialis descendens and transversus, pectoralis profundus, latissimus dorsi, trapezius pars thoracica and serratus ventralis thoracis and cervicis – supporting the hypothesis that excitation increases in the transition from walking to trotting (Fig. 4, Table 1). These same muscles showed significantly greater per-distance excitation in trotting than in walking, with the addition of the m. trapezius pars cervicalis. On a per-time basis, both the trapezius pars cervicalis and the omotransversarius muscles joined these muscles in showing greater excitation in trotting than in walking. Only the cleidobrachialis and the rhomboideus muscles failed to show any significant differences between walking and trotting. Like these differences in forelimb muscles, and in support of the excitation hypothesis, the external oblique showed significantly higher excitation per stride, per distance and per time in trotting than in walking.

Differences in instantaneous excitation between trotting and walking mainly reflected the per-stride excitation differences described above (Fig. 4). A few muscles, however, showed higher instantaneous excitation in walking than in trotting during part of the stride cycle. For example, the serratus ventralis thoracis and the external oblique muscles showed greater excitation in the second half of stance during walking.

Forelimb muscle excitation – trot *versus* gallop

Five extrinsic forelimb muscles had significantly lower per-stride excitation (EMG area or r.m.s.) in galloping than in trotting – pectoralis superficialis descendens and transversus, pectoralis profundus, and serratus ventralis thoracis and cervicis – refuting the hypothesis that excitation increases in the transition from trot to gallop (Fig. 4, Table 1). These same muscles also showed lower per-distance excitation in galloping, and were joined by the omotransversarius and the latissimus dorsi muscles, which declined in the leading limb. Two muscles showed the expected significant

increase in per-stride excitation, but only in the leading limb: the cleidobrachialis and the thoracic portion of the trapezius muscle. Excitation measured on a per-time basis was significantly greater in the m. cleidobrachialis and lower in the mm. serratus ventralis thoracis et cervicis in both leading and trailing limbs. The m. latissimus dorsi showed greater per-time excitation in only the trailing limb, and the pectoralis superficialis transversus muscle decreased whereas the thoracic portion of the trapezius muscle increased in the leading limb only. The external oblique muscle showed a decrease in excitation in the transition from trot to gallop; the trailing limb showed a decline in per-time excitation, and the leading limb showed a decline in per-stride, per-distance and per-time excitation. Differences in instantaneous excitation between trotting and galloping reflected the per-stride excitation differences described above.

Forelimb muscle excitation – leading *versus* trailing limb
Two extrinsic forelimb muscles had significantly higher excitation (EMG area or r.m.s.) in the leading forelimb than in the trailing forelimb on a per-stride, per-distance and per-time basis: the cleidobrachialis and the serratus ventralis cervicis (Fig. 4, Table 1). Three muscles showed the reverse, higher excitation in the trailing forelimb on a per-stride, per-distance and per-time basis: the pectoralis profundus, pectoralis superficialis transversus and external oblique.

In instantaneous excitation, the m. cleidobrachialis was greater in the leading limb around the time of lift-off, whereas the m. serratus ventralis cervicis was greater in the trailing limb at this time. The pectoralis profundus and pectoralis superficialis transversus muscles showed greater instantaneous excitation in the leading limb during two periods in the stride, stance and swing, indicating more lever-like action of the trailing forelimb than the leading forelimb. The rhomboideus muscle showed greater instantaneous excitation at the beginning of stance in the leading limb.

Hindlimb muscle timing
The majority of hindlimb muscles showed clear bursting patterns that were similar in walking, trotting and galloping, indicating that their basic functions were conserved across gaits.

Limb protractors – the tensor fasciae latae, cranial and caudal sartorius – were active at the end of stance and into swing (Figs 3, 5). The m. tensor fasciae latae showed a burst of activity centered around lift-off in all gaits. The cranial and caudal sartorius muscles were active at the end of stance and well into swing. The rectus femoris showed a pattern of activity that was divergent from the other hindlimb protractors. In addition to the second, smaller burst around mid-swing, consistent with limb protractor, the greater activity occurred at mid-stance or during the second half of stance, appropriate in timing to prevent passive hip extension. The rectus femoris was relatively inactive at lift-off compared with the other protractors.

Four muscles that are anatomically positioned to produce limb retraction – the gluteus superficialis and medius, semimembranosus and cranial biceps femoris – were active in the second half of swing and approximately the first 50–75% of stance (Figs 3, 5). Four muscles that can produce hindlimb retraction as well as knee flexion – the caudal biceps femoris, gracilis, semitendinosus and adductor magnus – showed a burst of activity around touch-down and lift-off.

Hindlimb muscle excitation – walk *versus* trot
Only four of the 12 extrinsic hindlimb muscles studied had significantly higher per-stride excitation (EMG area or r.m.s.) in

trotting than in walking – the tensor fasciae latae, caudal sartorius, gracilis and adductor magnus – supporting the hypothesis that excitation increases in the transition from walking to trotting (Fig. 5, Table 1). However, two muscles showed significantly lower excitation in trotting: the rectus femoris and cranial sartorius. The instantaneous excitation showed that the m. rectus femoris was more active at the end of stance in walking than in trotting, whereas the cranial sartorius muscle showed high activity already at the start of swing when the dogs walked. Per-distance excitation in trotting was greater for the tensor fasciae latae, caudal sartorius and gracilis muscles, but excitation was lower in the rectus femoris. Per-time excitation in trotting was greater in the tensor fasciae latae, caudal sartorius, gracilis, adductor magnus and semimembranosus muscles, but excitation was lower again in the rectus femoris.

Hindlimb muscle excitation – trot *versus* gallop
Ten of the 12 extrinsic hindlimb muscles studied had significantly higher per-stride excitation (EMG area or r.m.s.) in galloping than in trotting: the tensor fasciae latae, rectus femoris, sartorius cranial, gluteus superficialis, gluteus medius, semimembranosus, biceps femoris cranial, gracilis, semitendinosus and adductor magnus (Fig. 5, Table 1). The caudal sartorius muscle declined in excitation in galloping compared with trotting, whereas the m. biceps femoris caudal muscle remained unchanged. These results support the hypothesis of greater excitation in faster gaits. Per-distance excitation in galloping was greater for nine of the muscles that showed greater per-stride excitation (i.e. except the m. semitendinosus). Although the m. biceps femoris did not show any change, the caudal sartorius muscle declined in per-distance excitation in galloping compared with trotting. Differences in per-time recruitment were identical to per-stride excitation with the exception that the caudal sartorius muscle increased in excitation in galloping.

Hindlimb muscle excitation – leading *versus* trailing limb
Excitation in only two extrinsic hindlimb muscles could be compared in leading *versus* trailing limbs: the m. rectus femoris showed no differences in per-stride, per-distance or per-time excitation, whereas the m. semitendinosus showed significantly higher per-stride, per-distance and per-time excitation in the trailing limb (Fig. 5, Table 1).

Overall excitation
The extrinsic muscles of the forelimb and the hindlimb showed different changes in excitation between gaits. The majority of the forelimb muscles showed the greatest excitation in trotting *versus* in walking and galloping. In contrast, most of the hindlimb muscles showed the greatest excitation in galloping. The m. rectus femoris was unique in showing the lowest level of excitation in trotting. Excitation changes held for per-stride, per-distance and per-time excitation, and for muscles of different functional groups. The overall pattern shows that forelimb muscles tend to decline in excitation whereas the hindlimb muscles increase in the transition from trotting to galloping (Figs 4, 5, Table 1).

DISCUSSION
The goal of this study was to determine how the extrinsic limb muscles change in the timing of activity and excitation among gaits in dogs in order to detect possible functional differences of these muscles at different gaits. We focused on the proximal fulcra because they are important for force transfer between the limbs and the trunk. We expected the forelimb and hindlimb muscles to differ in part

because of the unique muscular sling of the forelimb (Davis, 1949; Gray, 1968; Gambaryan, 1974), which is particularly important in cursorial mammals such as dogs because no skeletal connection exists between the limb and the trunk (e.g. Howell, 1944; Hildebrand, 1962). We expected differences in the forelimb and hindlimb because their mechanics have been found to differ in trotting: the forelimb acts more like a strut, with the ground-reaction force vector passing near the fulcrum, whereas the hindlimb acts more like a lever, with ground-reaction forces passing farther from the fulcrum and the extrinsic muscles providing propulsive force (Gray, 1944; Carrier et al., 2008; Schilling et al., 2009; Lee, 2011). Differences in activation were also expected because the proportion of locomotor work performed by the forelimbs and hindlimbs differs in trotting and galloping (Gregersen et al., 1998). Accordingly, we found that basic muscle function as well as the strut-like behavior of the forelimb and the lever-like behavior of the hindlimb (with respect to the proximal fulcra) are conserved across gaits, but that excitation changes differentially in the forelimb and hindlimb muscles.

Forelimb muscle timing

The timing of the activity of the extrinsic muscles of the forelimb indicates that the forelimb is acting as a strut at the proximal fulcrum in all gaits. Anatomical forelimb protractors – the cleidobrachialis, pectoralis superficialis descendens and transversus, and omotransversarius muscles – likely initiate swinging of the limb and may prevent passive retraction of the forelimb at the end of stance, consistent with their inactivity during the first half of stance, and activity in all gaits in the final third of stance and into swing (Fig. 4). Activity of the forelimb retractors – the latissimus dorsi and pectoralis profundus muscles – in the second half of swing phase is consistent with them braking the swing of the forelimb at the end of swing at all gaits. The activity of the m. pectoralis profundus during stance of the trailing limb in galloping indicates that it may act in propulsion, in addition to its gait-independent function of limb retraction. The smaller bursts of activity in both the pectoralis superficialis descendens and transversus muscles at the end of swing are consistent with a retractor function of these muscles in braking the forelimb at the end of swing in addition to their protractor function. The relative sizes of the bursts associated with protraction and retraction of the three subdivisions of the m. pectoralis are consistent with progressively greater retractor function and less protractor function with increasing caudality of fiber orientation in the descendens, transversus and profundus portions, respectively (Fig. 4).

The activity of the m. serratus ventralis thoracis only during stance is consistent with this muscle acting as a muscular sling to support the trunk against vertical accelerations in all gaits, as has been found in dogs (Nomura et al., 1966; Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974; Carrier et al., 2006), cats (English, 1978), opossums (Jenkins and Weijs, 1979) and vervet monkeys (Schmitt et al., 1994).

Muscles that have been proposed to act as fulcrum stabilizers in trotting dogs (Carrier et al., 2006; Carrier et al., 2008) show similar patterns in all gaits, consistent with the conservation of this function. The bursting of the cervical trapezius muscle at the time of lift-off and touch-down is consistent with it stabilizing the fulcrum during reversals of limb movement in all gaits, as well as counteracting retraction at the end of stance and protracting the limb at the start of swing. The activity of the rhomboideus and serratus ventralis cervicis muscles centered around touch-down indicates a function in all gaits of stabilizing and defining the point of rotation of the scapula as the forelimb retractors become active at the end of swing and with the function of bracing the limb against impact forces that

tend to displace the scapula dorsocaudally in the first half of stance, confirming previous observations in cats (English, 1978).

The m. trapezius p. thoracica was unusual in that it showed different activity patterns among gaits relative to the footfall pattern of the ipsilateral limb, suggesting that its activity is influenced by contralateral limb position and motion. In the leading forelimb in galloping, the activity during the first half of stance may stabilize the fulcrum and prevent abduction of the scapula, which may occur because at this time no other limbs are on the ground (Fig. 2). Also, during the leading limb's swing phase, the contralateral forelimb has just touched down, so activity may be needed to support the scapula in the vertical direction and prevent the ipsilateral forelimb from prematurely touching down. This function of elevating the forelimb is consistent with experiments in which excitation increased when dogs wore wrist weights (Carrier et al., 2008). During the first half of swing phase of the trailing limb, the contralateral (leading) forelimb is in swing as well, so there is nothing causing trunk collapse to the ipsilateral side, but the contralateral forelimb touches down in the second half of swing, requiring activity on the ipsilateral side at this time to prevent premature touch down. Timing of the activity of the thoracic trapezius muscle in trotting shows an intermediate pattern between the pattern observed for the leading and trailing forelimbs, but coincides with the start of stance of the contralateral forelimb, again consistent with an elevation function. In both trotting and galloping, activity of the thoracic trapezius muscle in swing coincides with the start of stance of the contralateral forelimb. These combined patterns indicate that the m. trapezius p. thoracica acts to reduce movement of the scapula laterally during stance and dorsoventrally during swing.

The trunk muscle examined, the m. obliquus externus, showed biphasic and bilateral activity with bursts during the first half of stance and the first half of swing of the ipsilateral forelimb. The biphasic activity of the external oblique muscle is most evident in trotting and is appropriate to aid the rectus abdominis (Robert et al., 2001) and the internal oblique muscles (Fife et al., 2001) in counteracting trunk sagging. Although the activity of the external oblique muscle at the thoracic site that we recorded is appropriate for this anti-sagging function, previous experiments designed to increase sagging by loading the mid-trunk of trotting dogs showed no significant increase in the activity of the m. obliquus externus at an abdominal recording site (Fife et al., 2001). The difference in amplitude between the two bursts in each locomotor cycle indicates that the external oblique may have other functions (Wakeling et al., 2007; Schilling and Carrier, 2010). The larger burst of activity during ipsilateral stance is appropriate to stabilize the ribs against activity of the m. serratus ventralis thoracis associated with support against gravity (Carrier et al., 2006), and possibly stabilization of the trunk against torques induced by the extrinsic limb muscles (Fife et al., 2001). Finally, the timing of external oblique muscle activity is appropriate to reverse the lateral extension of the trunk during the symmetrical gaits, which is greatest around lift-off of the ipsilateral hindlimb (Jenkins and Camazine, 1977). Thus the biphasic activity of the m. obliquus externus may counteract trunk sagging, whereas the larger burst of activity during ipsilateral stance may stabilize the ribs against the activity of the m. serratus ventralis thoracis that supports the trunk against gravity during walking, trotting and galloping, and may produce lateral bending of the trunk during the symmetrical gaits.

Hindlimb muscle timing

The timing of the activity of the extrinsic muscles of the hindlimb indicates that the hindlimbs act as a propulsive lever at the hip in

all gaits. The majority of hindlimb muscles showed clear bursting patterns that were similar in walking, trotting and galloping, indicating that their basic functions are conserved across gaits. Activity of a protractor, the m. tensor fasciae latae, was centered around lift-off in all gaits and is consistent with a function of preventing passive limb retraction at the end of stance and initiating swing. In contrast, the cranial and caudal sartorius muscles showed activity at the end of stance and well into swing, which indicates that they function mainly in limb protraction and less in hip stabilization (Fig. 5). The m. rectus femoris is anatomically positioned to act as a protractor, so its activity in mid-swing can be interpreted as protracting the limb. Its greater activity in stance in galloping and walking, however, indicate antagonism to the limb retractors and implies a function in hip stabilization against passive extension. The lack of protractor muscle activity at the beginning of stance indicates that the small amount of braking performed at the hindlimb early in stance (e.g. Wentink, 1977; Budsberg et al., 1987; Rumph et al., 1994; Walter and Carrier, 2007) is accomplished by activity of hindlimb retractors, with the ground-reaction force vector passing in front of the proximal fulcrum rather than behind it (Gregersen et al., 1998).

Four hindlimb muscles that are positioned to produce limb retraction – the gluteus superficialis and medius, semimembranosus and cranial biceps femoris muscles – showed activity in swing that indicates their function in braking the swinging limb, and also showed activity in stance that indicates a propulsory function independent of gait. Four muscles that can produce hindlimb retraction as well as knee flexion – the caudal biceps femoris, gracilis, semitendinosus and the adductor magnus muscles – showed activity that is consistent with limb retraction at the end of swing and into stance, and with knee flexion at the end of stance at all gaits.

Forelimb muscle excitation

The majority of the extrinsic forelimb muscles showed the highest excitation in trotting compared with walking and galloping, including muscles from all functional groups: protractors, retractors, sling muscles and fulcrum stabilizers. These results support the hypothesis that excitation increases in the transition from walking to trotting, but refute the hypothesis that excitation is greatest in galloping. The forelimb does not appear to be producing active retraction, based on the inactivity of retractors during stance. The higher excitation of the pectoralis profundus, transversus and descendens muscles in trotting also reflects the shorter time duration of the swing phase in trotting, which requires higher acceleration and deceleration to initiate and end the swing phase, hence higher forces and muscle excitation than in walking and galloping. Interestingly, the same pattern was not observed in the hindlimb. However, the general pattern of the greatest excitation occurring in the forelimb muscles in trotting is reinforced by significant differences in additional muscles, such as the serratus ventralis thoracis and cervicis, when excitation is measured on a per-distance and per-time basis, indicating that the higher excitation in trotting is not simply caused by differences in stride length and duration among gaits but reflects changes in amplitude. These results agree with calculations of locomotor work in dogs based on ground-reaction forces (Gregersen et al., 1998), in which the forelimb performs more work than the hindlimb in trotting, but declines in its work output in galloping while the hindlimb increases its work output. The pattern also is consistent with greater collisional losses in trotting compared with galloping (Ruina et al., 2005; Bertram and Gutmann, 2009; Lee et al., 2011), energy

that presumably is absorbed by the muscular sling and fulcrum stabilizers as well as more distal muscles and tendons of the forelimb.

The two exceptions to the above pattern were the cleidobrachialis and thoracic trapezius muscles, which showed the highest excitation in the leading limb. The cleidobrachialis is active at the end of stance preventing passive limb retraction, and the thoracic trapezius prevents scapular abduction during stance. This level of excitation can be interpreted as a response to high load, because in galloping the leading forelimb is the only limb on the ground during its stance phase and thus bears the entire ground-reaction force.

When comparing leading and trailing forelimbs in galloping, a similar effect is seen in the rhomboideus and thoracic trapezius. Both showed higher instantaneous excitation in the leading limb (the only limb in stance) in the beginning of stance when they resist dorsocaudal displacement of the scapula, compared with excitation in the trailing limb, which is in stance simultaneously with the leading hindlimb (Fig. 4). Likewise, the cleidobrachialis and cervical serratus ventralis muscles showed higher excitation overall in the leading limb compared with the trailing limb, which acts to brace the forelimb during impact with the ground.

Excitation of the forelimb protractors and retractors also indicates that different forces are transmitted by the leading and trailing forelimbs. The instantaneous excitation of the pectoralis profundus and pectoralis superficialis transversus muscles was higher in the leading limb during stance, indicating more lever-like action of the trailing forelimb than the leading forelimb at the proximal fulcrum. However, both muscles also showed higher instantaneous excitation in the trailing limb during swing, which may be necessary for rapid protraction after the ipsilateral hindlimb touches down and pitches the trunk forward.

The proposed functions of the m. obliquus externus in counteracting trunk sagging are consistent with the significantly higher excitation on the side of trailing limb compared with the leading limb. Because no other limbs are on the ground during leading forelimb stance, trunk sagging cannot occur and excitation is lower than in the trailing limb. During this time, the activity of the m. serratus ventralis thoracis is also reduced, consistent with the internal oblique muscles stabilizing the ribs against the action of this sling muscle.

Hindlimb muscle excitation

In contrast to the excitation pattern in the forelimb, the majority of the extrinsic hindlimb muscles showed the highest excitation in galloping. This pattern was observed in most of the hindlimb retractors (on per-stride, per-distance and per-time bases) and supports the hypothesis that excitation increases in the transition from trotting to galloping as greater propulsive impulses are required.

Hindlimb protractors show a mixed pattern that indicates complex interactions among muscles. The caudal sartorius muscle is excited most in trotting, which is consistent with the shorter swing phase and correspondingly higher limb accelerations occurring in this gait. The cranial sartorius showed similar timing of activity; however, it is recruited more in walking and galloping than in trotting, suggesting that this muscle is not as important for initiating swing in trotting as the caudal sartorius. The m. rectus femoris is also activated most in walking and galloping, but the instantaneous excitation indicates that this difference occurs mainly during stance (Fig. 5), when this muscle would resist passive retraction of the hindlimb.

Concluding remarks

The timing of muscle activity indicates that the extrinsic muscles retain their basic functions (i.e. protractor, retractor, sling and fulcrum stabilizer) across gaits. The great similarity in the timing of activity in walking, trotting and galloping indicates that the forelimb acts primarily as a strut and the hindlimb acts primarily as a propulsive lever at the proximal fulcra in all gaits, in accord with our understanding of locomotor dynamics of mammals (Gray, 1968; Carrier et al., 2008). The strut-like action of the forelimb at the proximal fulcrum is also consistent with minimizing locomotor–ventilatory interference, which might occur if muscles that insert on the sternum and ribs (e.g. the m. pectoralis profundus or the m. serratus ventralis thoracis) were active in stance to produce active forelimb retraction (Carrier et al., 2006).

Extrinsic forelimb and hindlimb muscles show different patterns of change in their excitation level across gaits. Many forelimb muscles have the greatest activity in trotting, consistent with greater locomotor work done by the forelimb in trotting than in galloping (Gregersen et al., 1998). The leading forelimb in galloping – the only limb on the ground during its stance phase – shows the next highest level of activity and walking shows the lowest. The change in excitation across gaits is different in the hindlimb, with most of the muscles showing increasing excitation in the order walk–trot–gallop, consistent with an increasing propulsory role of the hindlimb and increasing impulses with increasing speed of locomotion.

The difference in excitation changes between forelimb and hindlimb muscles is also compatible with our understanding of the collisions of the limbs with the ground that redirect the body's center of mass from a downward to an upward trajectory (Ruina et al., 2005; Bertram and Gutmann, 2009). In trotting, the forelimbs and hindlimbs may share this function; however, in the transverse gallop the hindlimbs initiate this redirection. If the initiating hindlimb produces a greater propulsive impulse than the other limbs, it may be reflected in a disproportionate increase in excitation of the hindlimb retractors in gallop beyond that required simply by the increase in speed.

Our results show that with the change of gait – and thus increasing locomotor speed – excitation of extrinsic limb muscles increased due to both increased peak activity and changes in the duration of activity. Because scapular and femoral, or shoulder and hip joint, kinematics do not substantially change when dogs switch gaits (Goslow et al., 1981; Fischer and Lilje, 2011), the observed differences in activity are primarily the result of changes in duration of limb movement and peak forces. Axial bending in dogs is greater in galloping and can contribute to propulsion; however, the integrated activity of the epaxial muscles does not differ from that in trotting (Schilling and Carrier, 2010), indicating that the limbs are accounting for differences in propulsive impulses.

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