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Function of the epaxial muscles during trotting

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SUMMARY

In mammals, the epaxial muscles are believed to stabilize the trunk during walking and trotting because the timing of their activity is not appropriate to produce bending of the trunk. To test whether this is indeed the case, we recorded the activity of the m. multifidus lumborum and the m. longissimus thoracis et lumborum at three different sites along the trunk (T13, L3, L6) as we manipulated the moments acting on the trunk and the pelvis in dogs trotting on a treadmill. Confirming results of previous studies, both muscles exhibited a biphasic and bilateral activity. The higher burst was associated with the second half of ipsilateral hindlimb stance phase, the smaller burst occurred during the second half of ipsilateral hindlimb swing phase. The asymmetry was noticeably larger in the m. longissimus thoracis et lumborum than in the m. multifidus lumborum. Although our manipulations of the inertia of the trunk produced results that are consistent with previous studies indicating that the epaxial muscles stabilize the trunk against accelerations in the sagittal plane, the responses of the epaxial muscles to manipulations of trunk inertia were small compared with their responses when moments produced by the extrinsic muscles of the hindlimb were manipulated. Our results indicate that the multifidus and longissimus muscles primarily stabilize the pelvis against (1) vertical components of hindlimb retractor muscles and (2) horizontal components of the hindlimb protractor and retractor muscles. Consistent with this, stronger effects of the manipulations were observed in the posterior sampling sites.

Key words: electromyogram, EMG, *Canis*, longissimus, multifidus, trunk, mammals, dog.

INTRODUCTION

The axial muscles of mammals serve a number of different functions during locomotion. First, they produce movements of the spine that generate positive or negative external work (global mobilization). Second, they counteract, control or restrict movements that are either passively induced by gravitational and inertial forces, actively produced by antagonists, or transmitted to the trunk by the extrinsic limb muscles, i.e. they dynamically stabilize the trunk (global stabilization). Third, they ensure the integrity of the locomotor apparatus by linking the vertebrae, to allow the global muscles to act on larger units of the spine (local stabilization) (Schilling, 2009). The superficial and multisegmental muscles such as the m. multifidus or the m. longissimus have been shown to be well equipped to mobilize as well as to globally stabilize the spine because of their relatively high proportion of fast fibers whereas deep and oligosegmental muscles such as the mm. rotatores are well suited to locally stabilize the spine because of their higher proportion of slow fibers in both non-cursorial (e.g. Yokoyama, 1982; McFadden et al., 1984; Kojima, 1998; Schilling, 2009) and cursorial mammals (e.g. Carlson, 1978; Armstrong et al., 1982; Yokoyama, 1982; Strbnec et al., 2004; Acevedo and Rivero, 2006).

Because the activity patterns of the epaxial muscles during walking and trotting in mammals have been found not to be consistent with the production of trunk movements, most investigators have concluded that the epaxial muscles function to stabilize the trunk during symmetrical gaits (Carlson et al., 1979; English, 1980; Shapiro and Jungers, 1994; Licka et al., 2004). Nevertheless, the specific locomotor forces and moments that require this stabilization were not discussed. For example, the body axis needs to be stabilized against the inertial loadings that occur as the trunk is accelerated and decelerated in the fore–aft and vertical directions during each stride. Additionally, the trunk must be dynamically stabilized against the forces applied to it by the extrinsic muscles as the limbs (1) cycle through the accelerations of both swing and support phase and (2) apply forces to the trunk to accelerate the center of mass of the body. Finally, the epaxial muscles may stabilize the trunk in ways that allow lung ventilation. Hence, there are a number of possible stabilizing functions that epaxial muscles probably provide during walking and running, but currently the literature contains only a few observations that can help us resolve the function of the epaxial muscles. Our limited understanding of what the epaxial muscles do during locomotion is striking when it is contrasted with our relatively extensive knowledge of the locomotor function of limb muscles.

Only three studies have proposed specific hypotheses for the locomotor function of the epaxial muscles in symmetrical gaits. Ritter et al. (Ritter et al., 2001) and Robert et al. (Robert et al., 2001a) hypothesized that the epaxial muscles counteract sagittal rebound of the trunk during trotting. Because the trunk sags due to its inertia during the first half of a trotting step, it tends to rebound during the second half of the step. Both studies tested and confirmed this hypothesis by manipulating the inertial moment of the trunk by having the dogs carry additional mass on the trunk (Ritter et al., 2001) or having the horses run at a variety of speeds (Robert et al., 2001a). Although, the timing of the bilateral activity of the back muscles (i.e. simultaneous activity during the second half of stance and swing) is appropriate to restrict the ‘sagittal rebound’, in order to stabilize the trunk against sagittal movements one would expect bilaterally symmetrical activity. However, in a variety of mammals, the epaxial burst of activity ipsilateral to the stance limb is always larger than the burst contralateral to stance (Carlson et al., 1979; Shapiro and Jungers, 1994; Ritter et al., 2001; Robert et al., 2001a;

Robert et al., 2001b). This asymmetry in the activation of the epaxial muscles points to additional functional roles of the epaxial muscles beyond simply restricting sagittal rebound.

A second hypothesis is based on studies on cats (Wada et al., 2006). These investigators suggested that the epaxial muscles increase the stiffness of the vertebral column and produce medially directed forces to decrease lateral trunk excursions induced by limb action. During walking, the trunk periodically swings from side to side. In order to restrict lateral bending, activity can be expected on the side on which the trunk is extended, i.e. the side ipsilateral to hindlimb support. However, in their data, the larger pulse of the biphasic activity was recorded contralateral to hindlimb stance and thus would produce lateral bending rather than restricting it. Furthermore, the asymmetry in the activity pattern reported by Wada et al. (Wada et al., 2006) is different from patterns observed for other walking mammals including cats (Carlson et al., 1979; Shapiro and Jungers, 1994) in which the higher burst occurs during ipsilateral hindlimb stance.

These conflicting results raise questions about the functional role of the epaxial muscles during symmetrical gaits in mammals. To increase our understanding of the function of the epaxial muscles, we manipulated the locomotor forces acting on the trunk in dogs while they trotted on a treadmill. The locomotor forces were manipulated while the muscle activity of the two medial epaxials, the m. multifidus lumborum and the m. longissimus thoracis et lumborum, was recorded at three sites along the trunk.

MATERIALS AND METHODS

The activity of the m. longissimus thoracis et lumborum and the m. multifidus lumborum was monitored at three different cranio-caudal sites along the trunk (T13, L3, L6) in six mixed-breed dogs (*Canis lupus familiaris* Linnaeus 1758) while they trotted on a motorized treadmill at moderate speed (~$2\,\mathrm{m\,s^{-1}}$). The mean body mass of the three males and three females was 25±3 kg. All individuals were obtained from local animal shelters (UT, USA) and trained to trot on the treadmill unimpeded and under conditions of various force manipulations. Recordings started on the third or fourth day after the surgical implantation of the electrodes and continued for 5–6 days. The electrodes were removed no later than 10 days after implantation and, after a period of recovery, all dogs were adopted as pets. The study was carried out in parallel to recordings of the hindlimb protractor and retractor activity (Schilling et al., 2009) and therefore, the same experimental protocol and subjects were used in both studies. All procedures conformed to the guidelines of the University of Utah Institutional Animal Care and Use Committee (# 02-06014).

Instrumentation and recording

Surgical implantation of the electrodes, recording of the muscle activity, and data analysis were described in detail previously (Carrier et al., 2006; Carrier et al., 2008). Briefly, the dogs were initially anesthetized with Pentothal and intubated for artificial ventilation. Anesthesia was maintained with Isoflurane for the duration of the surgery. Incisions were made through the skin and the thoracolumbar fascia above the site of electrode placements. Sew-through electrodes (Basmajian and Stecko, 1962) were secured to the m. multifidus lumborum and the m. longissimus thoracis et lumborum at the level of and parallel to the spinous processes of T13, L3 and L6 using the same incisions for both muscles. The anatomy of the muscles is described in detail in Evans and we follow his nomenclature (Evans, 1993). The depth of the electrode placement within the muscles was approximately 0.5–1.0 cm. At each site, two electrodes were implanted to provide redundancy in case of electrode failure. Lead wires from the electrodes were passed subcutaneously to a site between the vertebral edges of the scapulae and exited the subjects slightly cranial to the shoulder blades in their neck.

Electromyographic (EMG) signals were sampled at 4000 Hz, filtered above 1000 Hz and below 100 Hz, and amplified approximately 2000 times. In order to correlate the locomotor events with the muscle activity, video recordings were made from a lateral view using a high-speed camera (60 Hz). An analog signal of the locomotor cycle was obtained by monitoring the vertical acceleration of the trunk with an accelerometer mounted to the dog's back. The video recordings were synchronized with the analog signals in order to associate the stride phases with the muscle recordings (for details, see Carrier et al., 2008).

Locomotor force manipulations

In order to improve our understanding of the locomotor function of the epaxial muscles, we monitored changes in the EMG patterns in response to defined manipulations of the locomotor forces. The following manipulations were applied as the dogs trotted at constant speed on the treadmill.

(1) To increase the vertical forces acting on the trunk, the dogs wore backpacks containing additional mass representing 0% (control), 8% and 12% of body mass. The masses were carried in three different positions on the back, representing three different trials: (i) the added masses were split up into two equal portions and carried over the pectoral and the pelvic girdles (pectoral and pelvic girdle mass); (ii) the mass was added to the middle trunk (mid-trunk mass); and (iii) the mass was carried over the pelvic girdle (pelvic girdle mass).

(2) To manipulate the fore and aft forces required to accelerate and decelerate the body, the treadmill was inclined so that the dogs ran both up- and downhill at slopes of 0 deg. (control), 10 deg. and 14 deg. from the horizontal. While running uphill, the incline increases the positive, propulsive work the dogs has to do in the fore–aft direction. While running downhill, the incline increases the negative, braking work the dogs had to do in the fore–aft direction. Additionally, the incline running altered the relative distribution of gravitational loads on the fore- and hindlimbs.

(3) To increase the forces necessary to protract and retract the hindlimbs during a running step, 0% (control), 1% and 2% of the dog's body mass were added to the hindfoot around the tarso-metatarsus.

(4) To manipulate the fore and aft forces, horizontally oriented forward- and backward-directed forces were applied to the dogs as they trotted on the level treadmill. Forward-directed forces were applied to the dogs with a handheld leash attached to a muzzle that required the dogs to resist the pulls by pushing backward as during braking. Rearward-directed forces were applied with a sled racing harness that applied the force to the chest region of the dogs, requiring the dogs to pull forwards against the harness. The muzzle was a greyhound racing muzzle which allowed the dogs to pant as they ran. The leash was attached to the front of the muzzle and the forces were applied *via* the occipital strap of the muzzle and thereby to the back of the head of the dogs. All applied horizontal forces were increased and decreased by manual manipulation and monitored with a force transducer that was in-series with the leash. The output of the force transducer was recorded digitally and displayed on an oscilloscope so that the experimenter could adjust the level of force.

During all force manipulations, the running speed was held constant during both the control and the experimental trials. The data for the different force manipulations were collected on different days and therefore, separate control trials were collected each day. During the controls, which were often performed before and after the manipulation, the dogs trotted unimpeded on the treadmill at the same speed as during the manipulations. Data from the different control trials collected during one session were used as an indicator of whether the dog's performance was influenced by muscle fatigue.

Analysis of the electromyographic signals

In order to examine the relationship between muscle recruitment and locomotor events and to facilitate comparisons among subjects and trials, time-normalized stride average EMGs were generated for each muscle and site from 20 strides of each dog (Banzett et al., 1992a; Banzett et al., 1992b; Carrier et al., 2006) (for details, see Carrier et al., 2008). The 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 the touchdown 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 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 or muscle site. The resulting stride average for each muscle or site was a series of 120 bins that represented the average activity of that muscle site during the stride.

The effect of the manipulations was illustrated by normalizing the amplitude of the EMGs of the experimental trial to the average amplitude of the controls. This normalization was performed in two steps. First, the average value for the 120 bins of the control trial was calculated. Then each bin of the control and manipulation trials was divided by this average control value. Once the data from each dog were normalized, the average bin values for the six dogs for both the force manipulation and the control were calculated. 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). The results are presented graphically as median and the lower and upper quartile (e.g. Figs 1–4). 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 2 and 3). The effect of the manipulation was also illustrated by plotting the difference between the control and manipulation signals as well as the 95% confidence interval (Figs 1–4). 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. Because we were able to collect and analyze data from both electrodes at each site of both muscles in all dogs (except T13 of m. multifidus lumborum and L6 of m. longissimus thoracis et lumborum), the presented data represent the results of both electrodes per site.

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 ± 1 s.e.m. (e.g. Table 1).

A similar analysis was undertaken to test whether the placement of the added mass that was above the girdles *versus* above the mid-trunk (manipulation 1), had an effect on the recruitment of the muscles. If there was no difference between the two manipulations, the result would be a ratio of 1. A ratio smaller than 1 would indicate a larger effect of the girdle masses on the muscle's activity whereas a ratio larger than 1 points to a higher effect of the mid-trunk mass on the recorded activity.

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, $P<0.05$) of the normalized EMG area against normalized force with all dogs included in a single regression.

In a previous study, the effect of the locomotor force manipulations on the metric parameters of the stride cycle was tested to check whether the force manipulations resulted in a change of the locomotor parameters. Only small or no changes in the stride phases were observed (Carrier et al., 2006; Carrier et al., 2008). In this study, we tested the effect of the inclined substrate (i.e. 10 deg. and 14 deg. up- and downhill) on the temporal parameters of the hindlimb stride cycle in the experimental trials in comparison to the control trials. For neither the swing nor the stance duration were the experimental trials significant different from the control trials.

RESULTS

M. multifidus lumborum

All three sites along the m. multifidus lumborum showed biphasic activity during the stride cycle when the dogs trotted at constant speed (Figs 1–4). The higher activity occurred during the ipsilateral hindlimb support and lasted approximately from mid stance to lift off (main burst). The second period of activity was correlated with the second half of the ipsilateral hindlimb swing phase and thus with the second half of the contralateral stance. The period of activity at all three sites along the trunk was mainly synchronized (i.e. the beginning and end of muscle activity but also the peak activity occurred at about same time during the stride cycle for all cranio-caudal sites).

Adding 8% or 12% of body mass to the limb girdles, the mid-trunk or the pelvic girdle had no significant effect on the activity of the multifidus muscle (Table 1; except one electrode at L6 when 8% of body mass was added). When the trotting dogs carried the added mass over their girdles *versus* over the middle of their trunk,

Table 1. Mean of the integrated area of the electromyograms of the manipulated trials presented as a proportion of the control trials for both electrodes at the respective vertebral levels of the m. multifidus lumborum and the m. longissimus thoracis et lumborum

Manipulation	Multi – T13	Multi – L3	Multi – L6	Long – T13	Long – L3	Long – L6
Pectoral and pelvic girdle mass						
8%	1.00±0.07 (6)	0.88±0.05 (6)	0.95±0.05 (6)	1.00±0.06 (5)	1.13±0.15 (6)	1.07±0.11 (5)
	0.95±0.03 (6)	0.91±0.02 (6)	0.98±0.06 (6)	0.94±0.05 (6)	1.00±0.05 (6)	1.16±0.08 (6)
12%	0.97±0.07 (6)	0.87±0.06 (6)	0.93±0.08 (6)	0.97±0.09 (5)	1.14±0.07 (6)	1.21±0.16 (5)
	0.92±0.04 (6)	0.90±0.05 (6)	0.96±0.09 (6)	0.98±0.04 (6)	1.06±0.06 (6)	1.39±0.19 (6)*
Mid-trunk mass						
8%	0.99±0.06 (5)	0.94±0.05 (6)	1.05±0.05 (6)	0.98±0.07 (5)	1.65±0.57 (6)	1.23±0.13 (5)
	1.00±0.04 (6)	1.00±0.22 (6)	1.05±0.03 (6)*	0.99±0.03 (6)	1.39±0.46 (6)	1.37±0.12 (6)
12%	0.99±0.07 (5)	0.77±0.16 (6)	1.07±0.05 (6)	1.01±0.09 (5)	1.30±0.36 (6)	1.33±0.16 (5)
	0.97±0.05 (6)	1.04±0.24 (6)	1.02±0.05 (6)	0.98±0.03 (6)	1.45±0.51 (6)	1.18±0.18 (6)
Pelvic girdle mass						
8%	0.78±0.06 (6)	0.80±0.07 (6)	0.88±0.06 (6)	0.75±0.10 (6)	1.31±0.33 (6)	1.14±0.13 (5)
	0.82±0.05 (6)	0.85±0.08 (6)	0.93±0.07 (6)	0.86±0.06 (6)	0.90±0.09 (6)	1.61±0.34 (6)
12%	0.75±0.11 (6)	0.70±0.07 (6)	0.94±0.07 (6)	0.71±0.13 (6)	1.09±0.19 (6)	1.25±0.08 (5)*
	0.79±0.08 (6)	0.82±0.13 (6)	0.88±0.07 (6)	0.85±0.08 (6)	0.83±0.09 (6)	1.31±0.21 (6)
Hills						
Uphill 10 deg.	1.22±0.14 (6)	1.40±0.14 (6)*	2.58±0.28 (6)*	1.12±0.14 (6)	1.94±0.49 (6)*	7.64±1.58 (6)*
	1.18±0.07 (6)*	1.53±0.16 (6)*	2.49±0.23 (6)*	1.46±0.11 (6)*	2.07±0.50 (6)*	7.30±1.99 (6)*
Uphill 14 deg.	1.30±0.18 (6)	1.53±0.14 (6)*	3.00±0.38 (6)*	1.33±0.46 (6)*	2.92±0.51 (6)*	9.58±2.51 (6)*
	1.22±0.08 (6)*	1.64±0.15 (6)*	2.96±0.39 (6)*	2.63±0.82 (6)*	2.83±0.80 (6)*	9.85±2.92 (6)*
Downhill 10 deg.	0.69±0.09 (6)*	0.64±0.07 (6)*	0.18±0.04 (6)*	0.67±0.10 (6)*	0.48±0.09 (6)*	0.21±0.10 (6)*
	0.73±0.10 (6)*	0.61±0.07 (6)*	0.22±0.07 (6)*	0.59±0.09 (6)*	0.40±0.07 (6)*	0.15±0.06 (6)*
Downhill 14 deg.	0.55±0.08 (6)*	0.54±0.05 (6)*	0.12±0.04 (6)*	0.68±0.43 (6)*	0.87±0.29 (6)*	0.43±0.35 (6)*
	0.65±0.11 (6)*	0.57±0.05 (6)*	0.14±0.05 (6)*	0.56±0.09 (6)*	0.44±0.10 (6)*	0.17±0.09 (6)*
Hindfoot mass						
1%	1.19±0.07 (6)*	1.25±0.06 (6)*	1.43±0.11 (6)*	1.34±0.08 (5)*	1.25±0.10 (6)*	1.91±0.24 (6)*
	1.19±0.07 (6)*	1.80±0.74 (6)	1.22±0.07 (6)	1.30±0.10 (6)*	1.27±0.11 (6)*	1.74±0.36 (6)*
2%	1.20±0.13 (6)	1.30±0.15 (6)*	1.29±0.12 (6)*	1.39±0.10 (5)*	1.41±0.16 (6)*	2.90±0.73 (6)*
	1.37±0.07 (6)*	2.21±0.88 (6)*	1.74±0.21 (6)*	1.51±0.09 (6)*	1.51±0.10 (6)*	2.22±0.50 (6)*

Multi, m. multifidus lumborum; Long, m. longissimus thoracis et lumborum.
Values are means ± standard error of change (number of individuals).
*Significant at $P<0.05$.

activity of the multifidus muscle was significantly higher in the mid-trunk trials in only four of the 12 comparisons (Table 2). The general characteristics of the activity were similar between control and trunk loading trials but the muscle activity was slightly delayed within the stride cycle in the manipulation trials (Fig. 1).

Running uphill on both the 10 deg. or 14 deg. inclined treadmill increased the activity of the multifidus muscle significantly at only one of the two electrodes at T13 but at all electrodes at the lumbar sites (Table 1). The increase in the muscle's activity was low at the thoracic sites (1.2- to 1.3-fold), somewhat more at the L3 sites (1.4- to 1.6-fold), and the most dramatic at the L6 sites (2.5- to 3-fold; Table 1). Whereas the timing of the two bursts during a stride cycle did not change in the posterior thoracic region (T13), a dramatic change in the period of the activity was evident in the lumbar region (Fig. 2). The beginning of the muscle's activity during ipsilateral stance was slightly delayed and the activity continued into the swing phase (up to the middle of ipsilateral swing at L6; Fig. 2). The same was true for the second burst, in which the activity lasted longer during ipsilateral swing at L3 and continued throughout touch down into the next ipsilateral stance phase at L6 (Fig. 2). Note that this shift increased at the more caudal sites (Fig. 2).

Running downhill at 10 deg. or 14 deg. significantly decreased the multifidus activity at all sampling sites (Table 1). Again, the response of the muscle was not similar at all cranio-caudal levels; rather the extent to which activity decreased when the dogs trotted downhill was more pronounced in the caudal recording sites (T13: 0.6- to 0.73-fold, L3: 0.5- to 0.6-fold, L6: 0.1- to 0.2-fold). The activity during ipsilateral stance started and ended earlier when running downhill in comparison to the controls, whereas the timing of the second burst during ipsilateral swing phase was uninfluenced by the manipulations in comparison to the control trials (Fig. 3). Note that the shift of the first burst during ipsilateral hindlimb stance was more pronounced in the most cranial site (T13) than the caudal one (L6).

In general, the addition of mass to the hindfoot increased the activity of the multifidus muscle at all recording sites although the change was not significant for one electrode at T13 for 2% and one electrode at L3 and L6 for 1% (Table 1). The effect of the

Table 2. Comparison of the integrated area of the muscle activity for both electrodes at the respective vertebral level of the m. multifidus lumborum and the m. longissimus thoracis et lumborum for all dogs when 8% or 12% of the body mass was carried above the mid-trunk *versus* split up and carried over the two girdles

Manipulation	Multi – T13	Multi – L3	Multi – L6	Long – T13	Long – L3	Long – L6
8%	1.00±0.02	1.07±0.06	1.12±0.10	0.95±0.04	1.31±0.22 *	1.14±0.07*
	1.05±0.04	1.13±0.08	1.09±0.07	1.05±0.03*	1.05±0.05	1.18±0.10
12%	1.03±0.04	1.10±0.08 *	1.20±0.14*	1.04±0.04	1.20±0.20	1.20±0.22*
	1.06±0.04*	1.13±0.05*	1.11±0.10	1.03±0.02*	0.97±0.07	0.91±0.17

Multi, m. multifidus lumborum; Long, m. longissimus thoracis et lumborum.

Values are means ± standard error of change. A mean change greater than 1 indicates that the activity was greater when the mass was carried over the mid-trunk.

*Significant at $P<0.05$.

manipulation was greatest at the most caudal lumbar sites with the two electrodes registering 1.3- and 1.7-fold increases in activity when 2% of the body mass was added (Table 3). The time course of the muscle's activity during a cycle was not influenced by the mass added. The raised base line between the main bursts in the lumbar sites, however, suggests a low level of a tonic activity throughout the step cycle (Fig. 4).

The application of horizontal fore or aft forces resulted in a significant response of the multifidus muscle at all cranio-caudal levels investigated (Table 3). During the forward pulls, i.e. when the dogs pushed backward and thus resisted being pulled forward, the integrated activity of the muscle decreased significantly with increasing force. When the dogs pulled forward against a backward directed force (i.e. backward pulls), the activity of the multifidus increased significantly as the applied force increased. Note that there was a cranio-caudal trend in the change of the muscle recruitment indicating a higher increase or decrease caudad (Table 3).

M. longissimus thoracis et lumborum

While the dogs trotted at constant speed on the horizontal treadmill, the longissimus muscle showed a biphasic activity pattern during a stride cycle (Figs 1–4). As was the case for the multifidus, the higher activity occurred during the ipsilateral stance phase and lasted from the middle of stance to lift off. The smaller activity was observed during the ipsilateral hindlimb swing and started in the second half of swing phase to last till touch down.

Adding mass to the trunk did not have a significant effect on the activity of the longissimus muscle (except one electrode at L6 with both a girdle or pelvic mass of 12%; Table 1). Adding mass to the trunk did not alter the general characteristics of the muscle activity but caused a slight delay in relation to the stride phases (Fig. 1). When the trotting dogs carried the added mass over their girdles *versus* over the middle of their trunk, activity of the longissimus muscle was significantly higher in the mid-trunk trials in only five of the 12 comparisons (Table 2). Nevertheless, when the results from both the multifidus and longissimus muscles were pooled, the average integrated activity of the six dogs was observed to be greater in the mid-trunk trials than in the girdle trials in 20 of the 24 comparisons. This higher activity in the mid-trunk trials was significant in a binomial distribution test (P=0.0006).

As in the multifidus muscle, activity of the longissimus muscle generally increased when the dogs trotted uphill and decreased when they ran downhill. In both situations, the changes were more dramatic in the caudal region of the trunk than the cranial site (e.g. 14 deg.: 1.3- to 2.6-fold at T13 *vs* 9.6- to 9.9-fold at L6). The changes were greater in the longissimus than in the multifidus muscles (Table 1). During running uphill, the changes in the activity of the longissimus muscle were significant for all sites except one electrode at T13 at 10 deg. (Table 1). The time course of the activity of the longissimus muscle changed during running uphill, especially in the lumbar region (Fig. 2). Whereas no change occurred at the thoracic site, the activity lasted from ipsilateral mid-stance until the first third of ipsilateral swing in the lumbar region. The second burst, which occurred during the second half of ipsilateral swing and ended around touch down during the control trials, lasted into the following stance phase. Thus, the longissimus muscle was continuously active around lift off and touch down of the ipsilateral limb in the lumbar region. When the dogs ran downhill at 10 deg. or 14 deg., the activity of the longissimus was significantly reduced at all sites along the trunk. While the muscle activity was reduced by about a third at T13, it was reduced to half of the activity during the control trials at L3 and exhibited only a third of the activity of the controls at L6 (Table 1). As was the case with the multifidus, the time course of the activity changed slightly during running downhill. Both, the main burst during ipsilateral swing and the second burst during swing started earlier in the stride cycle (e.g. L3 in Fig. 3).

Adding mass to the hindfoot caused a significant increase of the activity of the longissimus muscle at all recording sites independent of whether or not it was 1% or 2% of the body mass that was added. Comparing the thoracic and lumbar sites, the effect was greatest in the most caudal electrodes (L6; Table 1). The time course of the muscle activity during one stride cycle was not influenced by the added masses (Fig. 4).

The manipulation of the fore–aft forces caused a significant change of the integrated muscle activity at all cranio-caudal levels (Table 3). When the dogs were pulled forward *via* the muzzle and had to resist this pulling, the integrated activity of the longissimus muscle decreased significantly as applied force increased. When the dogs had to push forward against a rearward directed force, the integrated activity increased significantly with increasing force. Similarly to the m. multifidus, the changes were more dramatic in the caudal site than the cranial site (Table 3).

DISCUSSION

Both muscles investigated in this study showed biphasic and bilateral activity at all recording sites as the dogs trotted on a treadmill. The higher burst was always correlated with the second half of the ipsilateral hindlimb stance phase, the smaller burst occurred during the second half of the ipsilateral swing phase. The difference in these two bursts was noticeably greater in the longissimus than in the multifidus muscles. Our data confirm the results of previous studies on the activity pattern of the m. multifidus of walking cats (Carlson et al., 1979), baboons, chimpanzees, orangutans (Shapiro and Jungers, 1994) and trotting dogs (Ritter et al., 2001), as well as of the m. longissimus of walking cats (Carlson et al., 1979), primates (Shapiro and Jungers, 1994) trotting horses (Robert et al., 2001a; Robert et al., 2001b) and dogs (Tokuriki, 1973; Ritter et al., 2001). Our data are different in the timing of the activity for both muscles from trotting cats (English, 1980) and in the asymmetry of the two bursts per cycle from walking cats (Wada et al., 2006).

Stabilization in the sagittal plane

Previous studies have suggested that the function of the epaxial muscles during trotting in mammals is to control inertial oscillations of the trunk in the sagittal plane ('sagittal rebound hypothesis') (Ritter et al., 2001; Robert et al., 2001a). Although the results of trunk loading manipulations in this study are consistent with the previous experimental result of Ritter et al. (Ritter et al., 2001), in that we observed a significant increase in the activity of the epaxial muscles when added mass was carried over the mid-trunk, compared to when it was divided in half and carried over the girdles, the increase in activity due to mid-trunk loading was not as striking in this study as it was in the study by Ritter et al. (Ritter et al., 2001). The difference in the two studies may stem from higher running speeds and heavier trunk loads in the case of the Ritter et al. (Ritter et al., 2001) study. Nevertheless, in this study, we consistently observed more dramatic changes in epaxial muscle activity to manipulations of the protractor and retractor torques of the hindlimb than to manipulations of the inertia of the trunk.

As explained above, to produce or restrict sagittal bending, the epaxial muscles on both sides of the body are expected to be activated equally and synchronously to avoid a long-axis rotation of the trunk due to the oblique orientation of the muscle fascicles in the longissimus and especially the multifidus muscles (Evans, 1993). Nevertheless, the results of this study and of previous studies in various mammals show that the activity pulse ipsilateral to hindlimb support is always higher than the pulse during ipsilateral swing phase (Carlson et al., 1979; Shapiro and Jungers, 1994; Ritter et al., 2001; Robert et al., 2001b). The asymmetry in the two bursts leads to the suggestion that the epaxial muscles may do more in

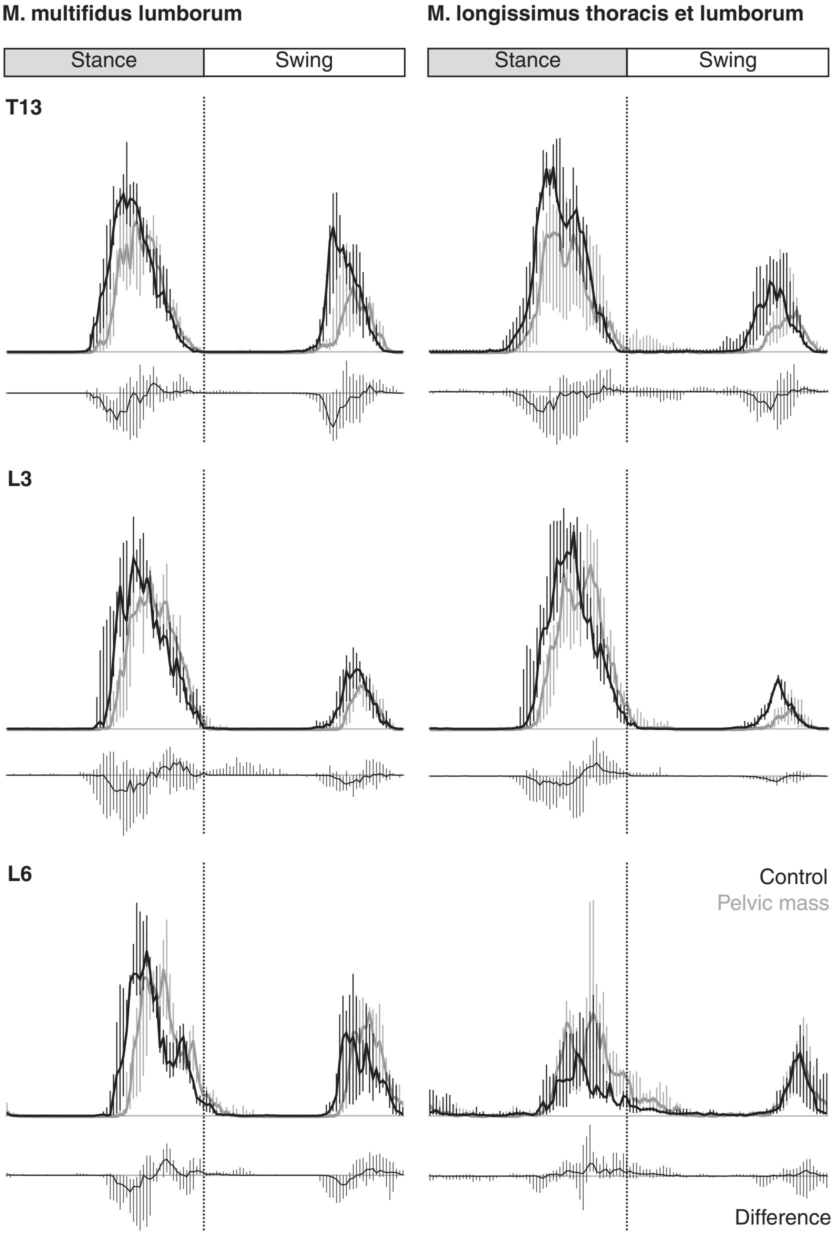

Fig. 1. Normalized electromyograms (EMGs) for control and manipulation signals as well as the difference between control and manipulation trials of the m. multifidus lumborum and the m. longissimus thoracis et lumborum from all six dogs when they trotted with 12% of their body mass carried in a backpack located over their pelvic girdle. 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 EMG 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 sampling window (bin). Note that control and manipulation signals were plotted relative to the maximum amplitude observed in the particular manipulation experiment. Thus, the relative amplitude of the control recordings for a given muscle varies (also in Figs 2–4). 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 cross 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 muscles or sampling sites.

trotting mammals then simply control inertial oscillations of the trunk in the sagittal plane.

Action of the hindlimb pro- and retractors induces retro- and anteversion of the pelvis, respectively, and thus sagittal extension or flexion of the spine (Gray, 1968). The main retractors of the hindlimb such as the gluteus medius, the semimembranosus, and the cranial portion of the biceps femoris muscles have been shown to be active in trotting dogs during the end of the ipsilateral swing phase to brake the forward motion of the limb and accelerate it caudad to initiate the stance phase (Schilling et al., 2009). To counteract anteversion of the pelvis and thus sagittal flexion of the trunk, which the retractors of the hindlimb would cause, the epaxial muscles have to be activated. But at the beginning of stance, when the femur is actively retracted and retractor muscle activity was recorded (Schilling et al., 2009), no activity, either ipsi- or contralateral, was recorded in the back muscles. At the same time, the trunk undergoes sagging due to the inertia of the trunk (Ritter et al., 2001). Therefore, we suggest that during level trotting the anteversion moment imposed on the pelvis by hindlimb retractor muscles at the initiation of stance phase is counteracted by the inertia of the trunk, rather than the epaxial muscles.

During trotting uphill, the recruitment of the hindlimb retractor muscles is dramatically increased (Schilling et al., 2009). At the same time, sagittal rebound of the trunk is reduced as more trunk weight is supported by compressive forces acting on the centra of the vertebrae and the intervertebral discs. Altogether, the increased retractor moment and the decreased inertial movements of the trunk result in an increased need for the epaxial muscles to stabilize the pelvis in the sagittal plane. The increased bilateral activity and especially the prolonged activity of both epaxial muscles are consistent with this increased need for stabilization (Fig. 1). With increasing inclination, both an increased activity level and a prolonged period of activity was also observed in the longissimus muscle of trotting horses (Robert et al., 2001b) and walking cats (Wada et al., 2006). The observation that the increased activity was more pronounced in the more caudal recording sites in the current

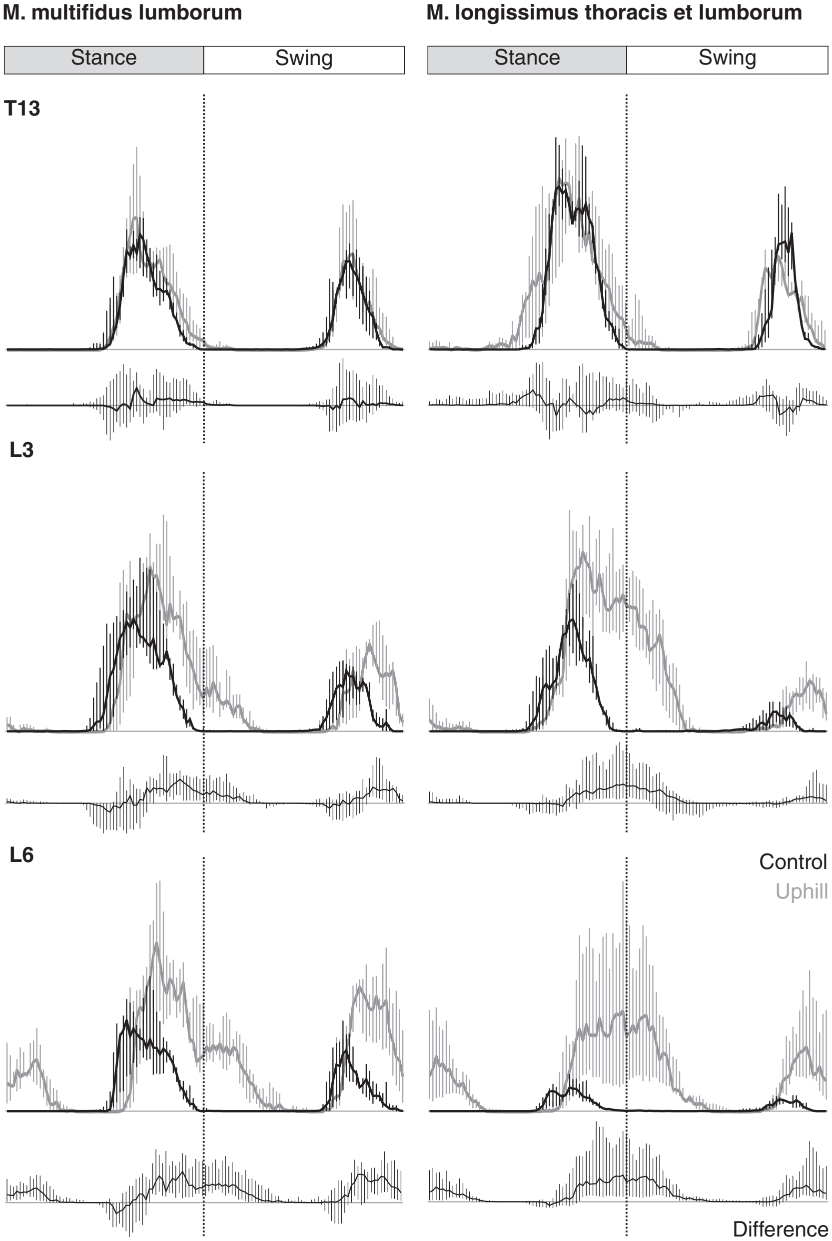

Fig. 2. Normalized EMGs for control and manipulation signals as well as the difference between control and manipulation trials of the m. multifidus lumborum and the m. longissimus thoracis et lumborum from all six dogs when they trotted uphill (14 deg.). For further explanation, see Fig. 1.

Table 3. Relationship between applied horizontal forces and EMG area for both electrodes at the respective vertebral levels of the m. multifidus lumborum and the m. longissimus thoracis et lumborum for all dogs

Manipulation	Multi – T13	Multi – L3	Multi – L6	Long – T13	Long – L3	Long – L6
Forward pull	–0.49 (0.32) <0.0001*	–0.50 (0.29) <0.0001*	–0.80 (0.70) <0.0001*	–0.45 (0.26) <0.0001*	–0.38 (0.17) <0.0001*	–0.45 (0.25) <0.001*
	–0.49 (0.32) <0.0001*	–0.41 (0.18) <0.0001*	–0.72 (0.56) <0.0001*	–0.44 (0.29) <0.0001*	–0.38 (0.19) <0.0001*	–0.53 (0.29) <0.0001*
Backward pull	0.55 (0.37) <0.0001*	0.63 (0.51) <0.0001*	0.68 (0.55) <0.0001*	0.05 (0.30) <0.0001*	0.53 (0.36) <0.0001*	0.73 (0.63) <0.0001*
	0.41 (0.20) <0.0001*	0.45 (0.30) <0.0001*	0.68 (0.57) <0.0001*	0.49 (0.28) <0.0001*	0.61 (0.44) <0.0001*	0.62 (0.50) <0.0001*

Multi, m. multifidus lumborum; Long, m. longissimus thoracis et lumborum.

Values are slope (R^2) and P value.

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 $P<0.05$.

study is also consistent with elevated retractor moments acting on the pelvis during running uphill. Similarly, when the dogs trotted with masses added to their feet, the hindlimb retractors have more breaking work to do at the end of swing. Thus, the increase of the epaxial muscle activity at the end of swing phase when mass was added to the hind feet is consistent with preventing sagittal flexion and anteversion of the pelvis at the end of swing. In this case also, the changes were more dramatic at the lumbar sites, i.e. closer to the pelvis.

Significant changes in the epaxial muscle activity were also observed when the horizontal forces acting on the dog were manipulated. Whereas epaxial muscle activity at all sites along the trunk decreased when the dogs were pulled forward *via* the muzzle, activity significantly increased when the dogs were pulled rearward wearing a harness. As expected, hindlimb retractor muscle activity also decreased when the dogs were pulled forward but increased significantly when the dogs were pulled rearward (Schilling et al., 2009). These results are consistent with the epaxial muscles functioning to stabilize the trunk and pelvis against anteversion torques imposed on the pelvis by the hindlimb retractor muscles.

During running downhill, retractor muscle activity is reduced to breaking the forward swinging of the limb at the end of swing phase. The reduced hindlimb retractor moment is consistent with the significantly reduced activity of both epaxial muscles. Whereas the activity at the thoracic site is only slightly decreased (to about two thirds), the decrease is more dramatic toward the caudal region of the trunk (to about one third at L6). Wada et al. (Wada et al., 2006) also reported a general decrease of the epaxial muscle activity in cats walking down a slope.

Activity of the protractor muscles of the hindlimb, such as the tensor fasciae latae or the cranial and the caudal sartorius muscles, mainly occurs before and during the first half of ipsilateral swing (Schilling et al., 2009). Action of the protractors exerts retroversion on the pelvis and would tend to extend the vertebral column. At the same time, when protractor muscle activity is observed, the trunk undergoes sagging due to its inertia, extending the back (Ritter et al., 2001). No activity of the epaxial muscles was observed during this phase of the stride cycle, presumably because it would increase sagittal extension. Protractor activity decreased when the dogs trotted downhill, most probably because gravitational forces effectively swing the limb forward, requiring less muscular work (Schilling et al., 2009). This may explain why no changes in the activity of the back muscles were observed. However, the extension of the back caused by both the inertia of the trunk and the protractor muscle activity is probably counteracted by abdominal wall muscles such as the m. rectus abdominis. The activity of this muscle has been shown to be appropriate to restrict trunk extension in trotting horses (Robert et al., 2001a).

Stabilization in the horizontal plane

Lateral bending of the trunk and associated pelvic rotations in the horizontal plane are ancestral locomotor characteristics of all vertebrates (Howell, 1944; Gray, 1968; Hildebrand, 1976). Based on their topography, the most laterally situated epaxial muscles (i.e. the mm. iliocostalis et longissimus) were thought to produce lateral bending movements (Slijper, 1946; Starck, 1978). In order to do so, ipsilateral and unilateral muscle activity, starting shortly before hindlimb lift off and continuing throughout swing phase can be expected. But, as shown for the longissimus in cats (Carlson et al., 1979), horses (Robert et al., 2001b) and dogs (this study) as well as for both the longissimus and the iliocostalis muscles in dogs (Ritter et al., 2001) and primates (Shapiro and Jungers, 1994), the main activity occurs during the second half of stance and ends prior to ipsilateral lift off. This pattern is inappropriate to produce lateral flexion, occurring during the period when the trunk laterally extends. Thus, the results of this study are consistent with previous results (Carlson et al., 1979; English, 1980; Shapiro and Jungers, 1994; Ritter et al., 2001), indicating that the main activity of both muscles investigated in this study is not consistent with the production of lateral bending.

The asymmetry of the bilateral activity of the epaxial muscles during a trotting step may be associated with the horizontal components of the moments imposed on the pelvis by the protractor and retractor muscles of the hindlimb. At the time in a step when one leg is at the end of swing phase and the other leg is at the beginning of swing, hindlimb retractors and protractors act simultaneously on the pelvis. That is, the m. tensor fasciae latae initiates the protraction of the hindlimb by its activity during the last third of stance while at the same time the retractors (mm. gluteus superficialis, gluteus medius, semimembranosus et biceps femoris) of the opposite hindlimb brake its forward swing and initiate its retraction (Schilling et al., 2009). The simultaneous action of protractor and retractor muscles would cause pelvic rotation about its dorsoventral axis and thereby lateral bending of the spine. Activity of the epaxials on the side of the body contralateral to the swinging leg, especially of the longissimus, could resist this pelvic rotation and lateral bending. Thus, asymmetrical activity of both epaxials in which the higher activity is contralateral to the swinging leg is consistent with stabilizing of the pelvis against rotation and thus against lateral bending. Increasing the protractor and retractor moments acting on the pelvis by adding mass to the hindfoot increased the activity of the epaxial muscles, particularly at the lumbar sites. This increased activity is consistent with an increased need to stabilize the pelvis in the horizontal plane.

During trotting uphill, when more work is required to laterally flex the trunk, the activity of the m. longissimus is significantly increased in comparison to the control trials and the primary burst is no longer limited to the ipsilateral stance. Instead, activity continues into the subsequent swing phase (L3, L6 in Fig. 2). Similarly, the activity on the other side of the trunk associated with ipsilateral swing continues into the consecutive stance phase and thus does not end with touch down. Although both epaxials investigated showed a significant increase in their activity during uphill running, the increased activity of the multifidus was largely bilaterally symmetrical, whereas the longissimus exhibited a clear asymmetry (L6 in Fig. 2). The longissimus exhibited substantially higher activity after ipsilateral lift off compared to its activity after the ipsilateral touch down. Because the timing of this unilateral increased activity in the longissimus muscle is consistent with the production of lateral flexion, we suggest, the longissimus muscle may assist in laterally bending the trunk during uphill running.

Stabilization in the transversal plane

Pelvic tilting, i.e. rotation about the anterior–posterior axis of the pelvis, is a plesiomorphic locomotor characteristic of all tetrapods. In trotting mammals, the pelvis is neutrally oriented along its long axis such that the two hip joints are at the same elevation at mid stance; whereas it is most tilted along its long axis at the point in step when one limb touches down and the other is lifting off (Jenkins and Camazine, 1977; van der Graaff et al., 1982; Schilling and Fischer, 1999). The ground reaction force exerted from the supporting limb causes a torsional moment on the pelvis that would tend to rotate it to the opposite side and thus twist the trunk. At the same time, the mass of the swinging leg is also acting to rotate the pelvis and trunk in the same direction. This tendency for the pelvis to rotate along its long axis could be resisted by activity of extrinsic hindlimb muscles such as the m. gluteus medius on the

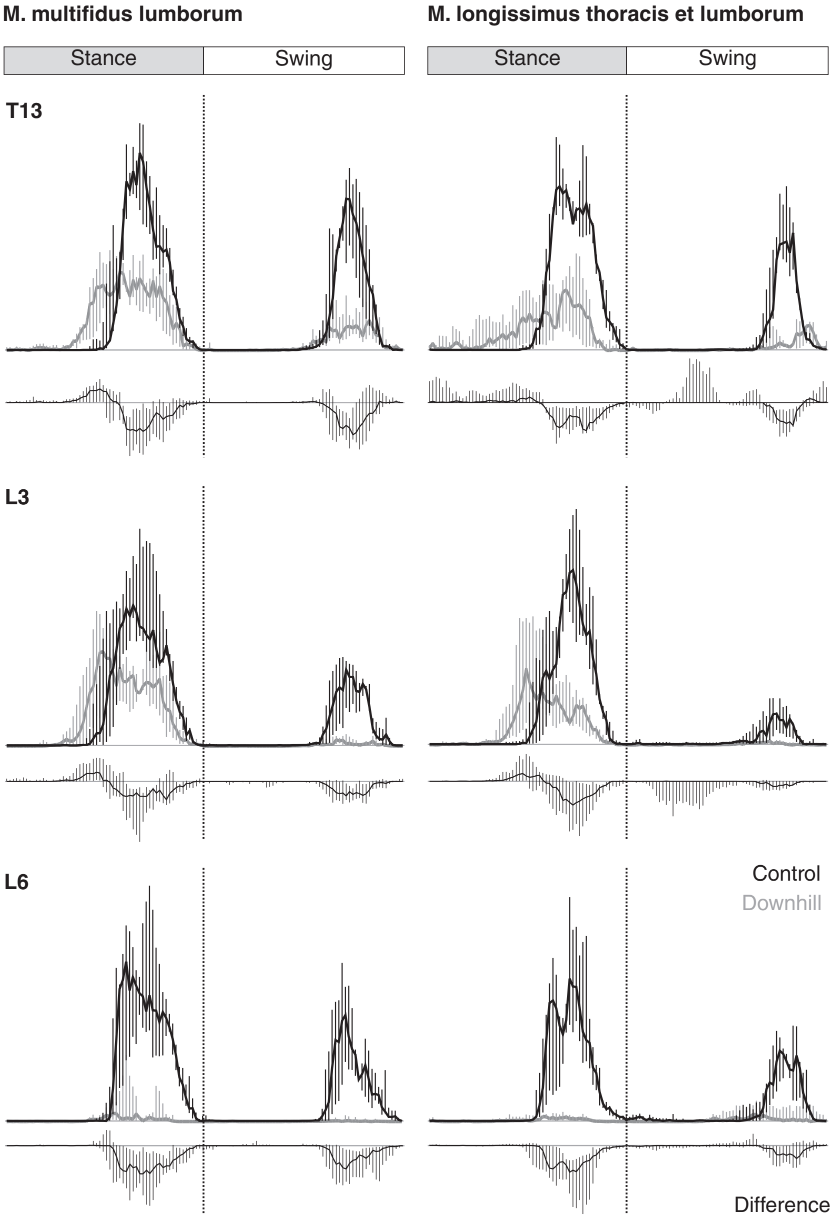

Fig. 3. Normalized EMGs for control and manipulation signals as well as the difference between control and manipulation trials of the m. multifidus lumborum and the m. longissimus thoracis et lumborum from all six dogs when they trotted downhill (14 deg.). For further explanation, see Fig. 1.

ipsilateral body side of the supporting leg (Schilling et al., 2009). Additionally, the oblique cranio-medial orientation of both the multifidus and the longissimus muscles (Evans, 1993) is well suited to counteract these torsional moments acting on the trunk. However, during level trotting, no activity in the epaxial muscles that was temporally consistent with long axis stabilization was recorded. Nevertheless, adding mass to the hindfoot is expected to increase the need for long axis stabilization during swing phase and did result in increased activity of both contralateral epaxials and particularly of the lumbar multifidus. Most striking, the caudal site of the multifidus showed tonic activity throughout the stride cycle (Fig. 4), which is consistent with a long axis stabilizing function of this muscle against forces transferred from the hindlimb onto the trunk *via* the pelvic girdle.

Conclusions

When dogs trot at constant speed on a level surface, the primary function of the lumbar epaxial muscles is to stabilize the trunk against the moments imposed on the pelvis by the extrinsic muscles of the hindlimb. The bilateral activity of the epaxial muscles during the second half of a trotting step is suggested to stabilize the pelvis against the vertical component of the moment imposed by hindlimb retractor muscles during the end of swing phase. The greater activity observed in the epaxial muscles ipsilateral to hindlimb stance phase is hypothesized to stabilize the pelvis against the horizontally oriented component of the moment on the pelvis induced by (1) action of the hindlimb protractor muscles initiating swing phase of the support limb and (2) action of the hindlimb retractor muscles ending swing phase of the ipsilateral limb. Although our manipulations of the inertia of the trunk produced results that are consistent with previous studies that indicated the epaxial muscles stabilize the trunk against accelerations in the sagittal plane (Ritter et al., 2001; Robert et al., 2001a), the response of the epaxial muscles to manipulations of trunk inertia were small compared to their response when moments produced by the extrinsic hindlimb muscles were manipulated. Finally, when dogs trot uphill or pull forward

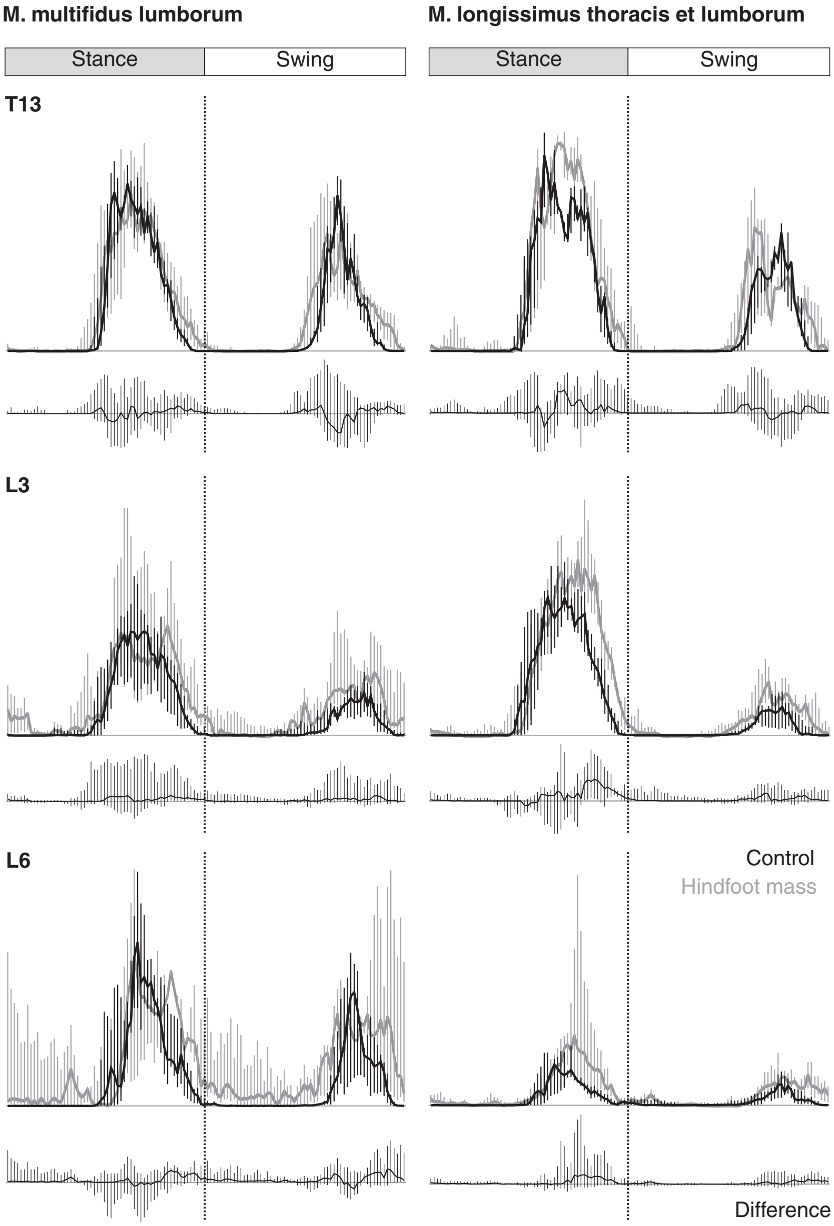

Fig. 4. Normalized EMGs for control and manipulation signals as well as the difference between control and manipulation trials of the m. multifidus lumborum and the m. longissimus thoracis et lumborum from all six dogs when they trotted with 2% of their body mass added to their hindfeet (except for T13 in m. longissimus thoracis et lumborum, N=5). For further explanation, see Fig. 1.

against a resisting force, the epaxial muscles exhibit elevated activity that is consistent with (1) stabilization of the pelvis against the increased moment imposed by the hindlimb retractor muscles and (2) assisting in the production of lateral bending of the trunk.

Although the m. multifidus lumborum and the m. longissimus thoracis et lumborum appear to function in trotting mammals to (1) globally stabilize the spine in all planes of the body, and (2) dynamically stabilize the pelvis against forces produced by the activity of the extrinsic hindlimb muscles, pelvic rotations in the horizontal plane and about the anterior–posterior axis of the pelvis do occur in both non-cursorial (van der Graaff et al., 1982; Pridmore, 1992; Schilling and Fischer, 1999) and cursorial mammals (Carlson et al., 1979; Jenkins and Camazine, 1977). Despite their relatively low amplitudes, horizontal and long-axis rotations of the pelvis may contribute to increasing step length and the production of locomotor work because the resulting pelvic motion is in the direction of body progression (Gray, 1968). Nevertheless, mammalian epaxial muscles are not involved in the production of lateral bending or tilting during level trotting. Rather, they seem to permit a certain amount of truncal motions. Whether other muscles such as the mm. psoas major et minor or the m. quadratus lumborum are actively involved in the production of these truncal movements or all spine motions during trotting are passively induced by gravitational forces and locomotor accelerations, or are caused by forces transmitted to the trunk by the extrinsic limbs muscles warrants further investigation.

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