

Function of the epaxial muscles in walking, trotting and galloping dogs: implications for the evolution of epaxial muscle function in tetrapods

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SUMMARY

The body axis plays a central role in tetrapod locomotion. It contributes to the work of locomotion, provides the foundation for the production of mechanical work by the limbs, is central to the control of body posture, and integrates limb and trunk actions. The epaxial muscles of mammals have been suggested to mobilize and globally stabilize the trunk, but the timing and the degree to which they serve a particular function likely depend on the gait and the vertebral level. To increase our understanding of their function, we recorded the activity of the *m. multifidus lumborum* and the *m. longissimus thoracis et lumborum* at three cranio-caudal levels in dogs while they walked, trotted and galloped. The level of muscle recruitment was significantly higher during trotting than during walking, but was similar during trotting and galloping. During walking, epaxial muscle activity is appropriate to produce lateral bending and resist long-axis torsion of the trunk and forces produced by extrinsic limb muscles. During trotting, they also stabilize the trunk in the sagittal plane against the inertia of the center of mass. Muscle recruitment during galloping is consistent with the production of sagittal extension. The sequential activation along the trunk during walking and galloping is in accord with the previously observed traveling waves of lateral and sagittal bending, respectively, while synchronized activity during trotting is consistent with a standing wave of trunk bending. Thus, the cranio-caudal recruitment patterns observed in dogs resemble plesiomorphic motor patterns of tetrapods. In contrast to other tetrapods, mammals display bilateral activity during symmetrical gaits that provides increased sagittal stability and is related to the evolution of a parasagittal limb posture and greater sagittal mobility.

Key words: back muscles, EMG, *Canis*, trunk, symmetrical gaits, asymmetrical gaits.

INTRODUCTION

The axial musculoskeletal system represents the ancestral engine of the vertebrate body. In tetrapods, body propulsion is dependent on concerted trunk and limb muscle action. In mammals, trunk motions are often less apparent than limb movements and the contribution of the trunk movements to body propulsion varies considerably with gait. Nevertheless, the body axis plays a central role in mammalian locomotion, because it contributes to the work of locomotion, provides the foundation for the production of mechanical work by the limbs, is central to the static and dynamic control of body posture, and integrates the coordinated actions of limbs and trunk (e.g. Howell, 1944; Gray, 1968; Hildebrand, 1959; Gambaryan, 1974; Starck, 1978). Considering its central role in locomotion, it is surprising how limited our understanding of the axial system is compared with our understanding of the limbs.

In mammals, the epaxial muscles are thought to serve several, potentially conflicting functions during locomotion (Schilling, 2009). First, they mobilize the trunk and thus can contribute to propulsion through the production of mechanical work (mobilization). Second, they control or counteract movements that are passively induced by gravitational and inertial forces, actively produced by antagonists, or transmitted to the trunk by extrinsic limb muscles; hence they dynamically stabilize the trunk (global stabilization). Third, they link the vertebrae and ensure the integrity of the spine, thereby allowing polysegmental muscles to act on larger units of the spine (local stabilization). Based on their topography, fiber type composition and recruitment pattern, the *mm. multifidus*

et *longissimus* have been suggested to mobilize as well as to globally stabilize the spine in all three planes of the body (Schilling, 2009; Schilling and Carrier, 2009). The degree to which they mobilize or dynamically stabilize the trunk during locomotion seems to depend on the gait performed (English, 1980) and the cranio-caudal location within the trunk (i.e. vertebral level) (Wakeling et al., 2007).

The locomotor gaits of mammals, such as walk, trot or gallop, differ strikingly in the body planes in which movements occur and moments act. Further, the amplitude of trunk movements varies substantially among the gaits and the cranio-caudal levels within the trunk. For example, during walking, trunk motions are restricted primarily to lateral bending and long-axis torsion (tilting), affecting the horizontal and the transverse planes of the body, respectively (e.g. Howell, 1944; Jenkins and Camazine, 1977; Graaff et al., 1982; Pridmore, 1992). Additionally, during trotting, the trunk undergoes low amplitude bimodal sagittal flexions and extensions due to vertical oscillations of the center of body mass (CoM) (Audigie et al., 1999; Ritter et al., 2001; Haussler et al., 2001; Robert et al., 2001). In contrast, the gallop is characterized by substantial unimodal dorso-ventral bending in the sagittal plane, i.e. with one flexion and extension per locomotor cycle (Howell, 1944; Hildebrand, 1959; Gambaryan, 1974). When mammals gallop, the amplitude of intervertebral movements increases cranio-caudally, implying a caudally increasing contribution to body propulsion (Schilling and Hackert, 2006). Further, lateral bending during walking and sagittal bending during galloping show a traveling wave, in which maximum excursion occurs in the anterior trunk region before the posterior

region (Pridmore, 1992; Kafkafi and Golani, 1998; Schilling and Hackert, 2006). In contrast, synchronized activation of the epaxial muscles points to a standing wave during trotting (Schilling and Carrier, 2009). Because the timing of limb cycling differs among the gaits, locomotor forces produced by extrinsic limb muscles, but also inertial and gravitational forces of the limbs, act on the trunk at varying times during the locomotor cycle. Vertical and horizontal components of extrinsic protractors and retractors induce sagittal extension and flexion, respectively, as well as lateral bending of the spine (Gray, 1968). Actions of the extrinsic forelimb muscles impact mostly the anterior trunk, while those of the extrinsic hindlimb muscles act primarily on the posterior trunk *via* the pelvic girdle (Virchow, 1907). In contrast, inertia of the CoM primarily affects the mid-trunk. Overall, the complexity of the various limb and trunk interactions, varying with gait and trunk region, hampers our understanding of epaxial muscle function during locomotion in mammals.

Among the different gaits, the trot has been investigated most intensively. In this gait, the epaxial muscles act to stabilize the trunk (1) in the horizontal and transverse planes against the horizontal components of extrinsic limb muscles and gravitational forces, respectively (Schilling and Carrier, 2009), and (2) in the sagittal plane against the inertia of the CoM ('sagittal rebound') (Ritter et al., 2001; Robert et al., 2001) and the vertical components of the extrinsic limb muscles (Schilling and Carrier, 2009). During galloping, muscle recruitment appears appropriate to extend the spine (Tokuriki, 1974; English, 1980). Several studies have investigated epaxial muscle activation patterns in different mammals at various gaits and at various vertebral levels. For example, activity of the *m. longissimus dorsi* in one dog was recorded at three vertebral levels (Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974). One study investigated cats at different gaits, but did not also quantify muscle recruitment (English, 1980); and three studies recorded the activity of the *m. longissimus dorsi* in walking or trotting horses but did not study asymmetrical gaits (Licka et al., 2004; Wakeling et al., 2007; Zaneb et al., 2009). No study, however, has systematically investigated epaxial muscle activation in the same species at different gaits and different vertebral levels.

The goal of this study was to assemble a more complete picture of the recruitment patterns of the epaxial muscles in different gaits to increase our understanding of the locomotor function of these muscles. Given the previous results on trunk kinematics and epaxial muscle function, we hypothesized that the epaxial muscles show (1) a distinctly asymmetrical and biphasic activity pattern during walking, (2) a less asymmetrical, biphasic activity during trotting, compared with walking (3) a symmetrical and monophasic recruitment during galloping, (4) synchronized activity along the trunk during trotting, and (5) sequential activation along the trunk during walking and galloping. To test these hypotheses, we recorded the activity of the *m. multifidus lumborum* and the *m. longissimus thoracis et lumborum* in dogs at three different vertebral levels along the trunk (thoracic: T13; lumbar: L3, L6) while they walked, trotted and galloped on a treadmill.

MATERIALS AND METHODS

The activity of two epaxial muscles, the *m. multifidus lumborum* and the *m. longissimus thoracis et lumborum*, was monitored at three different cranio-caudal sites along the trunk (T13, L3, L6) in six mixed-breed dogs (*Canis lupus f. familiaris*, Linnaeus 1758). Mean body mass of the three male and three female dogs was 25 ± 3 kg. The dogs performed three different gaits – walk, trot and gallop – while they moved on a motorized horizontal treadmill. Treadmill

speed was constant during the respective trials and gaits at approximately 1.4 m s^{-1} during walking, 2.3 m s^{-1} during trotting and 4.6 m s^{-1} during galloping. All dogs showed a lateral sequence walk; a trot, characterized by synchronized diagonal limb motions (Hildebrand, 1966); and a transverse gallop (Hildebrand, 1977) with a short common support phase of forelimbs or hindlimbs and a gathered suspension phase of all limbs (Figs 1–3). All six dogs performed for the trotting and galloping trials, but walking trials were recorded for only four of the dogs. Several galloping trials were recorded for each dog to enable analysis of muscle activity when the ipsilateral hindlimb acted as the trailing limb (i.e. the first one to touch the ground during a stride cycle) or when it was the leading limb (i.e. the second one touching the ground). Not all dogs switched trailing and leading hindlimbs, reducing the sample size to four for the gallop.

This study was carried out in parallel with previously published recordings of the epaxial and hindlimb muscle activity (Schilling and Carrier, 2009; Schilling et al., 2009). Therefore, the same experimental protocol and subjects were used. The dogs were obtained from local animal shelters in Utah (USA) and trained to perform on the treadmill unimpeded. Recordings started on the third or fourth day after the surgical implantation of the electrodes and continued for 5–6 days. The data for this study, however, were collected in one day. Electrodes were removed no later than 10 days after implantation and, after a period of recovery, all dogs were adopted as pets. All procedures conformed to the guidelines of the University of Utah Institutional Animal Care and Use Committee (no. 02-06014).

Instrumentation and recording

Surgical implantation of the electrodes, recording of the muscle activity and data analysis have been described in detail previously (Carrier et al., 2006; Carrier et al., 2008). Briefly, 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 through the skin and the thoracolumbar fascia for both muscles. The anatomy of the muscles has been described in detail by Evans and we follow his nomenclature (Evans, 1993). 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 neck, slightly cranial to the shoulder blades.

Electromyographic 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 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. Video recordings were synchronized with the analog signals to associate the stride phases with the muscle recordings (for details, see Carrier et al., 2008).

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 electromyograms (EMGs) were generated for each muscle, site and electrode from 20 strides of each dog (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 (i.e. ipsilateral to the operated side). 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-designed 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. 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 site was a series of 120 bins that represented the average activity of that muscle site during the stride.

To illustrate the effect of the different gaits on the EMG patterns, EMG averages were first amplitude-normalized using the average amplitude during trot. This normalization was performed in two steps. First, the average value for the 120 bins of the trot was calculated. Then each bin of the walk, trot and gallop trials was divided by this average control value. In contrast to the analysis performed in our previous study (Schilling and Carrier, 2009), in which the data for the two electrodes were presented separately, the time- and amplitude-normalized data from both electrodes per muscle and vertebral level were pooled in this study. For this, the time- and amplitude-normalized data from the two electrodes were averaged. Afterwards, the average bin values for the different dogs and the different gaits were calculated. By normalizing the values for each dog to mean trot activity prior to averaging across dogs, the pattern from one dog did not overwhelm the pattern from another (because of differences in EMG amplitude, for example). The results are presented graphically as median and lower and upper quartile (Figs 1–3). Note that the signals were plotted relative to the maximum amplitude observed at the respective vertebral level and gait plotted. Thus, the relative amplitudes are not directly comparable among each other in Figs 1–3.

To determine whether the intensity of muscle recruitment differed among the gaits, the sum of the bins recorded during a walking or a galloping stride was expressed as ratios of the sum of the bins of the trotting signals, respectively. We anticipated that recruitment would increase when dogs switched from a walk to a trot and increase further when they switched from a trot to a gallop. Thus,

we divided the sum of the bins of the trotting signal by that of the walking signal and divided the sum of the bins of the galloping signals (both trailing and leading limbs) by the trotting signal. In both cases, a ratio greater than 1.0 indicates that recruitment increased at a given electrode site when the dogs switched from a walk to a trot or from a trot to a gallop, respectively. These ratios were calculated using the pooled data from the two electrodes at each site and data were not normalized. A ratio of unity indicates that recruitment was not different in the two gaits; the null hypothesis. Means and 95% confidence intervals of these ratios were generated for each recording site and compared with the hypothesized ratio of 1.0 (e.g. Table 1). We assumed the results were significantly different from the null hypothesis if the 95% confidence intervals did not include 1.0.

We also tested whether the recruitment changes from walk to trot and trot to gallop were more pronounced in the mid-trunk (T13) or the posterior lumbar region (L6). For this, we divided the trot/walk ratio of T13 by that of L6 and the gallop/trot ratios of T13 by those of L6. No cranio-caudal difference in the recruitment change would result in a ratio of 1.0; the null hypothesis. Means and 95% confidence intervals of these ratios were generated for each recording site and compared with the hypothesized ratio of 1.0. We used one-tailed Wilcoxon signed-rank tests to determine whether the changes were different between T13 and L6. We hypothesized a greater change at T13 when the dogs switched from a walk to a trot but a greater change at L6 when the dogs switched from a trot to a gallop. Because the sample size for these comparisons was 4 dogs, we set the limit for significance at $P < 0.10$.

A similar analysis was undertaken to test whether the onset and offset of muscle recruitment varied cranio-caudally along the trunk. The onset and offset of the activity were determined by finding the time in the stride at which the EMG activity crossed an amplitude threshold of 0.5 of the mean activity for the recording site for more than 4% of the stride duration (i.e. 5 bins). Mean and 95% confidence intervals were generated for each muscle and all dogs. Then, we used Wilcoxon signed-rank tests to determine whether the times of onset and offset were different between T13 and L3 and between L3 and L6. We hypothesized that there would be a cranio-caudal sequence in the onset and the offset of the epaxial muscles during walking and galloping, but that onset and offset would occur more or less synchronously along the trunk during trotting. Thus, we used one-tailed tests for significance for the walk and trot and a two-tailed test for the trot. When the sample size was 5 or 6 dogs, we assumed the timing at the two sites was different when the P -value was less than 0.05. When the sample size was 4 or fewer, the timing was different when the P -value was less than 0.10 (Table 2).

Table 1. Integrated areas of the electromyograms of the walking and galloping trials (from 20 strides per dog) presented as ratios of the trotting trials (i.e. walking/trotting and trotting/galloping) at the respective vertebral levels of the m. multifidus lumborum and the m. longissimus thoracis et lumborum

	Multi – T13	Multi – L3	Multi – L6	Long – T13	Long – L3	Long – L6
Walk	4.57 (4)*	2.98 (4)*	2.02 (4)*	6.75 (4)*	5.36 (4)*	2.02 (4)
(Walk/trot)	3.48–5.66	2.64–3.31	1.06–2.97	1.01–12.49	2.44–8.28	0.46–3.57
Gallop	0.81 (4)	0.70 (4)*	1.34 (4)	0.67 (4)*	0.73 (4)	2.09 (4)
(Trot/trailing)	0.55–1.07	0.54–0.97	0.81–1.87	0.45–0.89	0.31–1.16	0.40–3.77
Gallop	1.06 (4)	1.08 (4)	1.21 (4)	0.92 (4)	0.69 (4)	2.02 (4)
(Trot/leading)	0.71–1.41	0.65–1.50	0.73–1.69	0.44–1.40	0.34–1.05	–0.02–4.06

Note that the epaxial muscle activity was higher during trotting than during walking, particularly at mid-trunk (T13). When the dogs galloped, epaxial muscle activity decreased or changed only slightly at T13 and L3 but increased at L6.

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

Values are mean and number of individuals in parentheses (first line); lower and upper confidence intervals (second line).

*Significant at $P < 0.05$.

Table 2. Onset and offset of the activity of the m. multifidus lumborum and the m. longissimus thoracis et lumborum as percentages of the stride cycle when the threshold was set at 50% of the mean activity as well as difference in timing of the onset or offset between adjacent recording sites

	Multi – T13	Multi – L3	Multi – L6	L3–T13	L6–L3
Walk on	20.8 (4)*	26.3 (4)*	29.0 (4)*	5.4*	2.7*
	12.8–28.9	21.1–31.4	23.7–34.2		
Walk off	46.9 (4)*	52.7 (4)*	62.1 (4)*	5.8*	9.4
	44.1–49.7	45.2–60.2	47.6–76.5		
Trot 1st on	22.5 (6)	23.2 (6)*	25.3 (6)	0.7	2.1*
	17.7–27.3	18.8–27.6	20.2–30.4		
Trot 1st off	43.1 (6)	45.0 (6)*	45.2 (6)	1.9*	0.8
	40.6–45.5	42.9–47.2	42.5–47.8		
Trot 2nd on	75.3 (6)	76.2 (6)*	76.3 (6)	2.8	1.7
	68.0–82.6	65.3–87.1	65.6–87.0		
Trot 2nd off	93.3 (6)	97.7 (6)*	95.3 (6)	3.5	–1.4
	89.2–97.4	86.9–108.5	93.0–97.7		
Gallop trailing on	60.2 (4)	61.0 (4)*	67.3 (4)	0.8	6.3*
	43.5–77.0	43.7–78.4	54–81		
Gallop trailing off	14.7 (3)	20.8 (2)*	16.1 (3)	–	–
	8.6–69.4	17.4–24.3	6–26		
Gallop leading on	30.4 (4)	35.8 (4)*	53.5 (4)	5.4*	17.7*
	27.4–33.4	32.8–38.9	49–58		
Gallop leading off	72.9 (4)	75.4 (4)	84.2 (4)	2.5	8.8*
	69.4–76.5	70.3–80.5	80–88		
	Long – T13	Long – L3	Long – L6	L3–T13	L6–L3
Walk on	20.0 (4)*	26.7 (4)*	33.1 (4)*	6.7*	6.5
	13.3–26.7	21.9–31.4	28.1–38.1		
Walk off	46.0 (4)*	52.9 (4)*	61.9 (4)*	6.9*	9.0
	43.3–48.7	46.2–59.6	46.2–77.6		
Trot 1st on	21.4 (6)	23.5 (6)	27.1 (6)	2.1	3.6*
	16.9–25.8	19.2–27.8	23.0–31.1		
Trot 1st off	44.6 (6)	46.1 (6)	47.7 (5)	1.5*	2.0
	42.5–46.7	44.4–47.8	42.4–52.9		
Trot 2nd on	77.4 (6)	76.7 (5)	78.5 (4)	1.0	3.8
	68.74–86.0	66.7–86.6	69.9–87.2		
Trot 2nd off	92.9 (6)	92.3 (5)	96.7 (5)	–0.2	4.3
	91.7–94.2	89.2–95.5	94.3–99.0		
Gallop trailing on	66.5 (4)	67.9 (4)	77.5 (4)	1.5*	9.6*
	56.7–76.2	59.5–76.4	71.7–83.3		
Gallop trailing off	15.4 (4)	20.2 (4)	26.7 (4)	4.8	6.5*
	11.0–19.9	15.4–25.0	24.4–29.0		
Gallop leading on	36.0 (4)	34.2 (4)	57.5 (4)	–1.9	23.3*
	27.2–44.9	28.0–40.3	52.4–62.6		
Gallop leading off	73.3 (4)	77.9 (4)	95.4 (4)	4.6*	17.5*
	69.4–77.2	72.0–83.8	86.9–104.0		

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

Values are mean and number of individuals in parentheses (first line); lower and upper confidence intervals (second line).

*Significant at $P < 0.05$ for $N > 4$ and at $P < 0.10$ for $N \leq 4$.

To infer whether a net extensor moment (bilateral activity) or a net lateral bending/torsional moment (unilateral activity) dominated (Wakeling et al., 2007), we compared the activation at the ipsilateral side with the activity that can be assumed to occur at the opposite side of the body at a respective vertebral level. Note that the inferred net-moment may not result in a movement in the particular body plane. Although epaxial activity was recorded from only one side of the body, Figs 1 and 2 provide an illustration of the assumed activity on the other side of the body during walking and trotting. To do this, we assumed symmetry in limb and trunk action. Activity of the epaxial muscles on the two sides of the body has been shown to be more or less identical during symmetrical gaits, but 180 deg. out of phase (Licka et al., 2004). Thus, to illustrate the activity on the two sides of the body, we shifted the recorded activity by 50% of the stride cycle (Hildebrand, 1966) to superimpose it with the actual recording. This way, the synchronization and the symmetry

or asymmetry between the two sides of the body were illustrated (Figs 1 and 2). Note that we recorded from only one body side per dog and that the superimposition with the 180 deg. phase shift of the recording was done solely to illustrate the pattern on the contralateral side of the body during locomotion at symmetrical gaits. For the gallop, the activity recorded ipsilateral to the leading hindlimb was aligned with recordings ipsilateral to the trailing hindlimb according to their timing of the footfalls (Fig. 3). Thus, for the gallop, mean signals from actual recordings from different trials are illustrated.

To compare the level of muscle recruitment, the same threshold as in the previous analysis was applied. Then, the sum of the bins for both bursts observed at the respective vertebral levels during the symmetrical gaits (except T13 and L3, where only one burst occurred during walking) and ratios between the activity at the ipsilateral and the 'contralateral' body sides were calculated. For

the gallop, the sum of the bins of the main bursts for the body side with the hindlimb acting as the trailing and the leading limbs, respectively, and the ratio between the two body sides were calculated. A ratio of 1.0 indicates symmetrical activity and thus a net extensor moment, while a ratio greater than 1.0 points to a net lateral bending/extensor moment and a greater asymmetry in the muscle recruitment between body sides. This analysis was only performed for the median activity calculated for all dogs because of the low sample size.

RESULTS

M. multifidus lumborum

When the dogs walked or trotted, the *m. multifidus lumborum* showed a biphasic activity pattern during the stride cycle (Figs 1 and 2). The greater activity (main burst) was associated with the second half of the ipsilateral hindlimb stance and the lower level activity occurred during the ipsilateral hindlimb swing phase. This biphasic activity pattern was clearly more pronounced during trotting than during walking. All recording sites showed a distinct second burst during trotting and a less pronounced asymmetry of the bilateral activity level compared with the walk. Superimposition of the recorded signal, to illustrate the assumed contralateral activity, shows that this asymmetry was somewhat more pronounced at L3 than at T13 or L6 (Fig. 2). At L3, the first burst was on average 3.8 times greater than the second one, while the main activity was 2.0 times greater than the second burst at the mid-trunk and only 2.2 times greater than the second burst at L6.

When the dogs walked, the posterior site (L6) showed a distinct second burst of activity, while this second burst was very small at T13 and L3 (Fig. 1). In contrast to the pattern during trotting, the amplitude of the second burst at L6 was as great as that of the first burst. Furthermore, the main activity showed two peaks at T13 during walking, of which only the second peak coincided with the main burst at the lumbar sites (Fig. 1). During trotting, however, all recording sites showed only one peak during their main burst of activity (Fig. 2).

Cranio-caudally, all three recording sites showed more or less simultaneously activity during trotting, i.e. activity at T13, L3 and L6 started and ended at roughly the same times during the stride cycle (Fig. 2). A significant difference in timing was only observed between the two lumbar sites at the beginning and between T13 and L3 at the end of the main burst (Table 2). In contrast, the muscles exhibited a sequential activation along the trunk during walking (Fig. 1). This was particularly true for the main burst (Table 2).

Compared with walking, the activity at all sampling sites increased significantly when the dogs trotted (Table 1). The greatest increase occurred at the most cranial recording site (T13), while the lowest increase was observed at the most caudal site (L6). This gait-associated change in EMG activity at T13 was significantly greater than the change at L6.

When the dogs galloped, monophasic activity was observed at all recording sites (Fig. 3). Muscle activity started at approximately the middle of the ipsilateral hindlimb swing phase and lasted throughout the subsequent stance phase when the ipsilateral hindlimb was the trailing limb. When the ipsilateral hindlimb functioned as the leading limb, the activity began after lift off and lasted throughout the swing phase. Nevertheless, superimposing the activity from the leading and trailing limbs shows that the activity occurred simultaneously during the stride cycle, resulting in a synchronized bilateral activity (Fig. 3). Activity on the leading body side was only slightly greater than that on the trailing body side at T13 and L3 (ratios T13, 1.4; L3, 1.6; L6, 1.0). At all vertebral levels, the

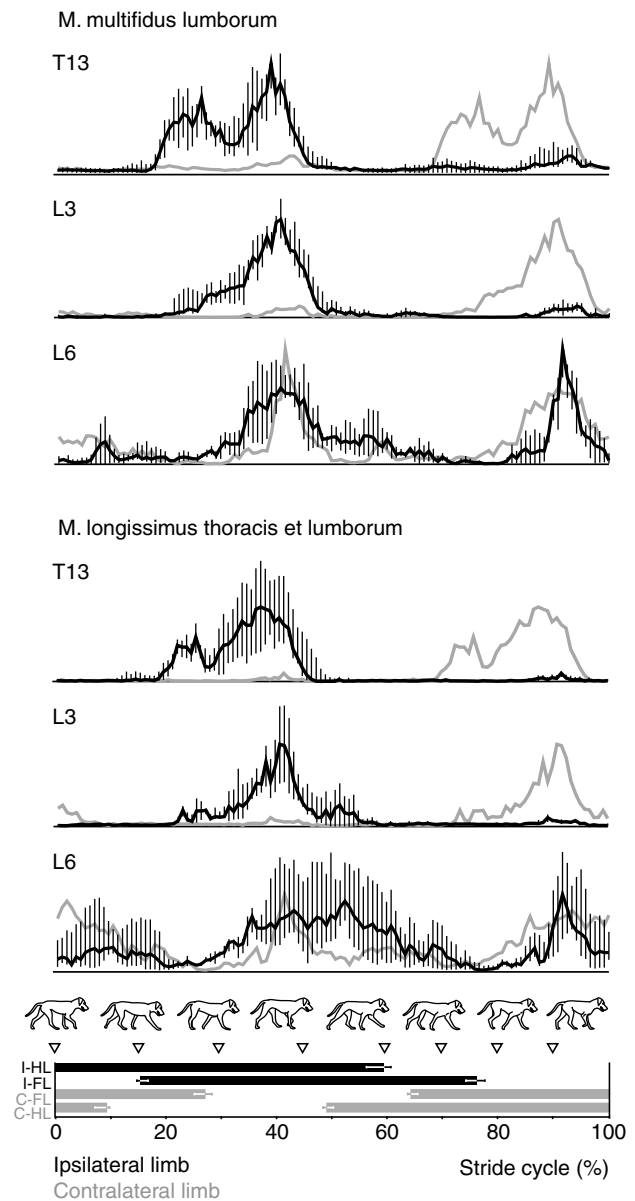


Fig. 1. Walk: normalized electromyograms (EMGs) (median plus upper and lower quartiles for each sampling window, i.e. bin, for 20 strides) of the *m. multifidus lumborum* and the *m. longissimus thoracis et lumborum* at the three cranio-caudal recording sites (T13, L3 and L6) when the dogs walked ($N=4$). Note that the signals are plotted relative to the maximum amplitude observed in the respective recording site. Thus, the relative amplitudes are not directly comparable. The x-axis represents the stride cycle beginning with the touch down of the ipsilateral hindlimb. The footfall pattern refers to the ipsilateral hindlimb (I-HL), ipsilateral forelimb (I-FL), contralateral forelimb (C-FL) and contralateral hindlimb (C-HL). Triangles above the footfall pattern indicate the timing of the corresponding posture of the dog illustrated by the above traces. Note that the EMG traces recorded at the ipsilateral body side (in black) are shifted by 50% of the stride cycle to illustrate the hypothesized activation on the contralateral body side (in gray) and the synchronization between the two sides.

monophasic activity consisted of two peaks. Of these, the second and smaller peak occurred just prior to the touch down of the leading hindlimb and the trailing forelimb (Fig. 3).

During galloping the *m. multifidus lumborum* was activated sequentially along the trunk (Table 2). This pattern was most obvious ipsilateral to the leading hindlimb (Fig. 3).

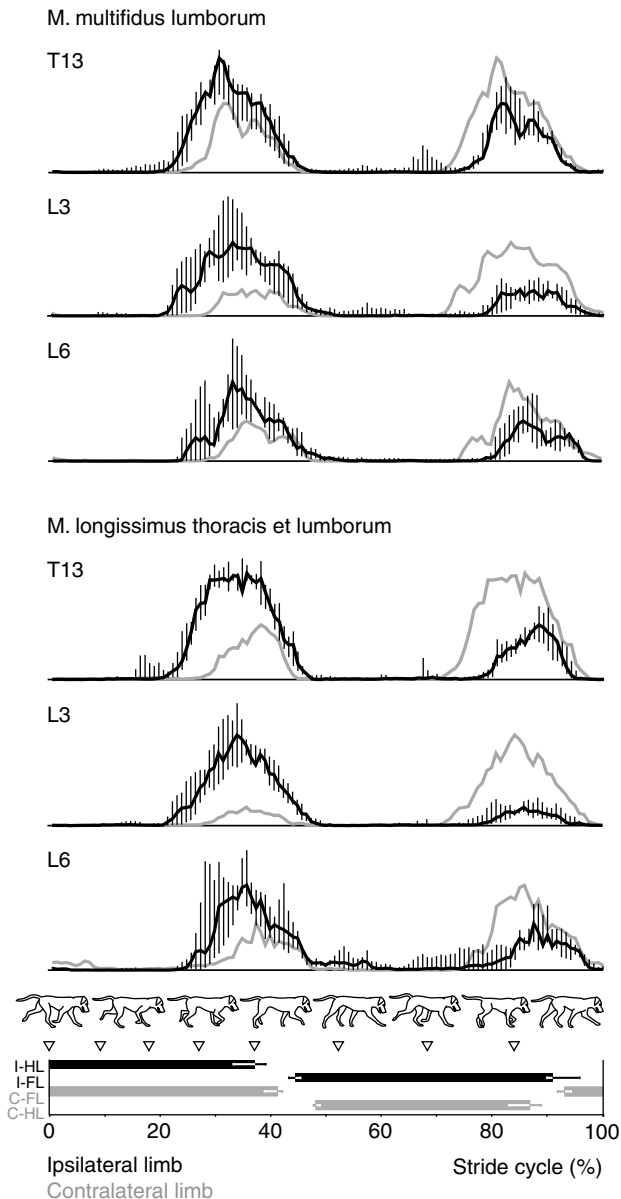


Fig. 2. Trot: normalized EMGs (median plus upper and lower quartiles for each sampling window, i.e. bin, for 20 strides) of the *m. multifidus lumborum* and the *m. longissimus thoracis et lumborum* at the three cranio-caudal recording sites (T13, L3 and L6) when the dogs trotted ($N=6$). Note that the signals are plotted relative to the maximum amplitude observed in the respective recording site. Thus, the relative amplitudes are not directly comparable. The x-axis represents the stride cycle beginning with the touch down of the ipsilateral hindlimb. The footfall pattern refers to the ipsilateral hindlimb (I-HL), ipsilateral forelimb (I-FL), contralateral forelimb (C-FL) and contralateral hindlimb (C-HL). Triangles above the footfall pattern indicate the timing of the corresponding posture of the dog illustrated by the above traces. Note that the EMG traces recorded at the ipsilateral body side (in black) are shifted by 50% of the stride cycle to illustrate the hypothesized activation on the contralateral body side (in gray) and the synchronization between the two sides.

The activity tended to be slightly higher during galloping than during trotting. This difference, however, was not significant ipsilateral to the leading hindlimb (Table 1). When the ipsilateral hindlimb was the trailing limb, the activity at T13 and L3 was lower during galloping than during trotting but higher at L6

(significant only for L3; Table 1). Interestingly, independent of whether the ipsilateral hindlimb acted as the trailing or the leading limb, the activity increased the most at L6; although this increase in recruitment was not significantly different from the increase at T13.

M. longissimus thoracis et lumborum

Similar to the *m. multifidus lumborum*, the *m. longissimus thoracis et lumborum* typically showed a biphasic activity pattern during walking and trotting (Figs 1 and 2). The higher activity was correlated with the second half of ipsilateral hindlimb support, whereas the second burst, if present, occurred during the last third of ipsilateral hindlimb swing phase. During trotting, all three recording sites showed two distinct bursts (Fig. 2) and the asymmetry between them was greater than the asymmetry in the *m. multifidus lumborum* (ratio of integrated area of first to second burst: T13, 3.4; L3, 7.4; L6, 2.5). When the dogs walked, the second burst of activity was as great as the main burst at L6 but much smaller at T13 and particularly small at L3 (ratios: T13, 13.5; L3, 19.9; L6, 2.2; Fig. 1). As was the case in the *m. multifidus lumborum*, the main burst at T13 contained two peaks in the *m. longissimus thoracis et lumborum*.

Along the trunk, the three recording sites exhibited a sequential activation of the muscle when the dogs walked but this difference in timing was only significant for T13/L3 (Table 2). All sites were activated more or less synchronously when the dogs trotted. However, a significant difference in timing was observed only at the beginning of the main burst for L3/L6 and in its ending at T13/L3.

Compared with walking, the integrated muscle activity of the *m. longissimus thoracis et lumborum* increased when the dogs trotted (significant for T13 and L3; Table 1). Similar to the *m. multifidus lumborum*, the greatest increase in muscle recruitment occurred at the mid-trunk (T13) and this gait-associated change in activity was significantly greater at T13 than at L6.

During galloping, the *m. longissimus thoracis et lumborum* exhibited monophasic activity with two pronounced peaks (Fig. 3). When the hindlimb acted as the trailing limb, the ipsilateral back muscle activity started around mid-swing and lasted throughout the subsequent stance phase. In contrast, activity occurred only during ipsilateral swing when the hindlimb was the leading limb. Aligning the activity patterns from the trailing and the leading hindlimb shows that the activity of the *m. longissimus thoracis et lumborum* is synchronized and largely symmetrical on the two sides of the body (Fig. 3). Muscle recruitment on the trailing body side was slightly greater than that on the leading side in the lumbar recording sites but this trend was reversed in the thoracic site (ratios: T13, 1.3; L3, 0.9; L6, 0.8). Similar to the pattern observed in *m. multifidus lumborum*, a second peak was observed at L6 in the *m. longissimus thoracis et lumborum* towards the end of the main activity. As was the case in the *m. multifidus lumborum*, activity of the *m. longissimus thoracis et lumborum* ipsilateral to the leading hindlimb preceded the activity ipsilateral to the trailing limb at T13 and L3.

Cranio-caudally, a sequential activation was observed when the dogs galloped. The thoracic site showed activity before the anterior lumbar site followed by the posterior lumbar site (Fig. 3). The cranio-caudal difference in the beginning and the end of the activity was significant for all recording sites (except the ending of the ipsilateral activity to the trailing hindlimb and the beginning of the activity ipsilateral to the leading hindlimb at T13/L3, Table 2).

Compared with trotting, the muscle activity was smaller at T13 and L3 but twice as great at L6 when the dogs galloped, independent

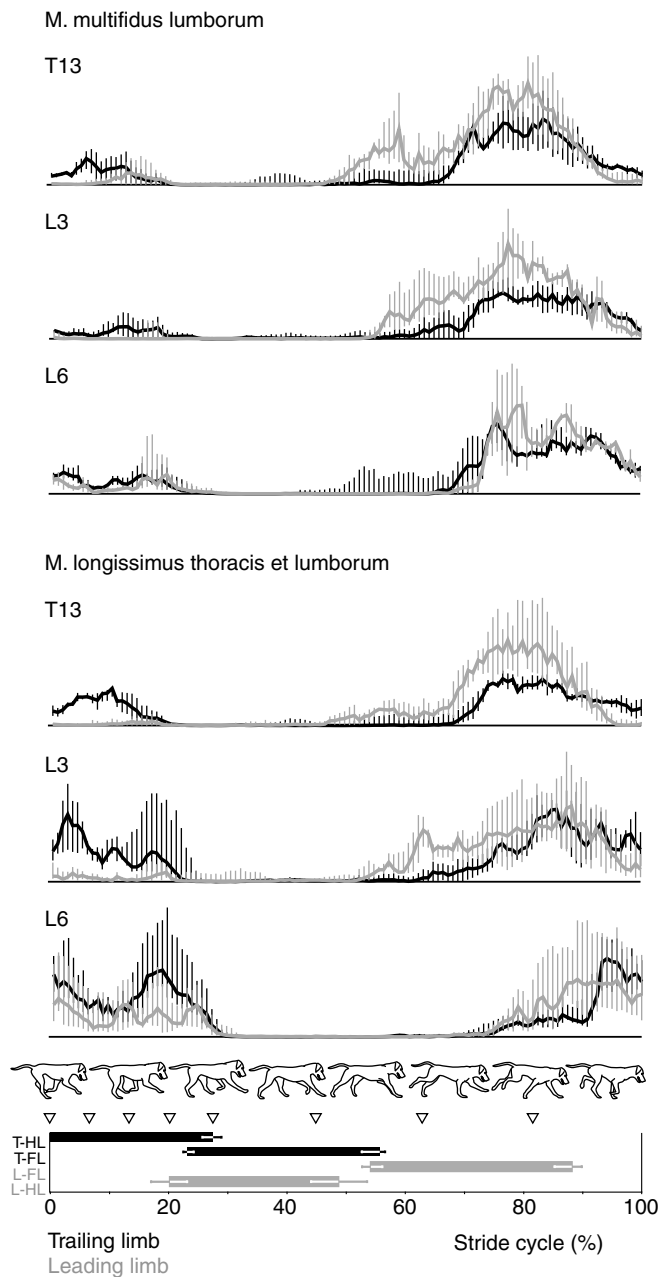


Fig. 3. Gallop: normalized EMGs (median plus upper and lower quartiles for each sampling window, i.e. bin, for 20 strides) of the *m. multifidus lumborum* and the *m. longissimus thoracis et lumborum* at the three cranio-caudal recording sites (T13, L3 and L6) when the dogs galloped ($N=4$). Note that the signals are plotted relative to the maximum amplitude observed in the respective recording site. Thus, the relative amplitudes are not directly comparable among sites. The x-axis represents the stride cycle beginning with the touch down of the trailing hindlimb. The footfall pattern refers to the trailing hindlimb (T-HL), trailing forelimb (T-FL), leading forelimb (L-FL) and leading hindlimb (L-HL). Triangles above the footfall pattern indicate the timing of the corresponding posture of the dog illustrated by the above traces. EMG traces associated with the trailing hindlimb are in black and those associated with the leading hindlimb are in gray.

of whether the ipsilateral hindlimb acted as the trailing or the leading limb (significant only for T13; Table 1). The recruitment change, however, was not significantly different between T13 and L6.

DISCUSSION

Hypotheses of the function of the epaxial muscles can be inferred from their topography and their patterns of activation. Because of their oblique fascicle orientation and their position relative to the neutral axis of the spine, epaxial muscle activity will result in moments in at least two planes of the body. Based on recruitment symmetry (i.e. bilateral activity) or asymmetry (i.e. unilateral activity) between the two sides of the body, a net extensor or net lateral bending/torsional moment can be inferred, respectively (Wakeling et al., 2007). A net extensor moment is expected if sagittal forces dominate (e.g. due to vertical oscillations of the CoM or vertical components of the extrinsic limb muscles). In this case, the main function of the epaxials would be to stabilize the trunk in the sagittal plane. Conversely, unilateral or pronounced bilateral asymmetrical activity is expected if lateral bending and torsional moments dominate. Then, the epaxial muscles would primarily function to laterally bend and/or twist the trunk or to stabilize it in the horizontal and/or transverse plane.

Both epaxial muscles investigated appear to provide mobilization and global stabilization in all three planes of the body. First, they produce bending in the horizontal plane during walking and trotting, and bending in the sagittal plane during galloping (mobilization). Second, they dynamically stabilize the trunk in the horizontal plane against the horizontal components of extrinsic limb muscle action, and in the sagittal plane against the sagittal components of limb muscle action and vertical oscillations of the CoM (global stabilization). Furthermore, they stabilize the trunk against long-axis torsion induced by gravitational and inertial forces. Thus, the two functions, mobilization and global stabilization, are not mutually exclusive. For example, unilateral activity may produce lateral bending towards the ipsilateral body side, may counteract lateral bending towards the contralateral side, or do both at the same time. Our results indicate that all these functions are accomplished by the epaxial muscles during the course of a locomotor stride, but the extent to which they serve a particular function varies with and depends on the animal's gait and the vertebral level.

Epaxial muscle activity during walking

When the dogs walked, recruitment of both epaxial muscles studied differed among the vertebral levels. Biphasic and bilateral activity was observed for the most caudal recording site (L6), as has been observed previously in the lumbar region of cats (Carlson et al., 1979; English, 1980; Zomlefer et al., 1984). In contrast, a nearly monophasic activity, associated with the second half of ipsilateral hindlimb stance phase, was recorded at the thoracic (T13) and the mid-lumbar (L3) sites. Similarly, Tokuriki reported a monophasic activity at T9 and a biphasic pattern at L4 for the *m. longissimus dorsi* in his dog (Tokuriki, 1973a). Cranio-caudal differences in the activation pattern were also described for the *m. longissimus* in horses (Wakeling et al., 2007) and the *m. erector spinae* in humans (de Seze et al., 2008). A correlation between the vertebral level and recruitment pattern may explain the variability in the epaxial muscle activity reported for primates (Shapiro and Jungers, 1994).

Muscle activity at the respective vertebral levels was synchronized between the two sides of the body in dogs (Figs 1 and 2), horses (Wakeling et al., 2007) and humans (de Seze et al., 2008). Muscle recruitment, however, was distinctly asymmetrical at T13 and L3 in the dogs, which points to a net lateral bending/torsional moment at these vertebral levels, while the more symmetrical activation at L6 implies a somewhat greater extensor moment. Accordingly, a

greater role for lateral bending and torsional moments was reported for the cranial compared with the caudal recording sites in the *m. longissimus dorsi* in walking horses (Wakeling et al., 2007). Likewise, distinct asymmetry in muscle recruitment between the two body sides was also reported for walking humans (de Seze et al., 2008).

Is the asymmetrical activity on the two body sides due to a need to produce or resist lateral bending or is it in response to a need to stabilize the trunk against long-axis torsion? If the two epaxial muscles function to produce lateral bending during walking, muscle activity is expected to be coincident with or precede the maximum lateral flexion on the contralateral side of the body. During a walking step, the pelvis rotates in the horizontal plane, alternately moving one hip joint anterior of the other. Maximum pelvic rotation is associated with the touch down and lift off events (Jenkins and Camazine, 1977). Therefore, maximal lateral flexion of the presacral region is associated with the end of the ipsilateral hindlimb swing phase, while maximum lateral extension occurs around ipsilateral lift off. The timing of the activity recorded close to the pelvic girdle (L6) is consistent with the production of lateral bending in that both epaxial muscles showed activity shortly before ipsilateral touch down. Furthermore, the main burst started during the second half of stance and lasted into the first half of swing and thus would be appropriate to reverse the pelvic rotation and initiate the subsequent lateral flexion after lift off. Because lateral bending in walking mammals resembles a traveling wave (i.e. lateral flexion in the anterior trunk region precedes the lateral flexion in the posterior region) (Pridmore, 1992; Kafkafi and Golani, 1998; Haussler et al., 2001), a cranio-caudal shift in the activity should be observed along the trunk. In accordance with a traveling wave, the onset and offset of the main burst of the epaxial muscle activity occurred at T13 before L3 and at L3 before L6. Furthermore, the asymmetry between bursts, resulting in a net lateral bending moment, is consistent with the production of bending. A cranio-caudal order in the offset of the main burst was also found in the *m. longissimus dorsi* in walking horses and, as observed here, the cranio-caudal pattern was more pronounced in the thoracic than in the lumbar region (Wakeling et al., 2007). Even though their trunk motions are primarily rotations about the long-axis of the body, humans, interestingly, also show a cranio-caudal order of muscle activation in their *m. erector spinae* during walking (de Seze et al., 2008).

In quadrupedal mammals, long-axis torsion can be expected to be greatest when one or both limbs of one body side are in swing phase and the body tends to collapse to that side. Muscle activity on the contralateral side of the body is expected if the epaxial muscles functioned to resist long-axis rotation. The greater ipsilateral activation at all vertebral levels and particularly the nearly unilateral activity at T13 and L3, that coincides with the swing phases of the contralateral forelimbs and hindlimbs (Fig. 1), would be appropriate in timing to stabilize the trunk in the transverse plane.

In addition to their role in the production of lateral bending and in long-axis stabilization, the two epaxial muscles investigated also stabilize the trunk against locomotor forces produced by extrinsic limb muscle action (Schilling and Carrier, 2009). Accordingly, the impact of these locomotor forces is greater close to the limb girdles than at the mid-trunk. For example, hindlimb protractor and retractor muscles induce rotations of the pelvis and thus lateral and sagittal bending of the spine (Gray, 1968). The horizontal components of both the protractors ipsilateral to the supporting limb and the retractors of the contralateral side cause a horizontal moment on the pelvis that must be counteracted by unilateral epaxial muscle activity ipsilateral to the hindlimb in stance (Schilling and Carrier,

2009). Consistent with stabilization against the horizontal components, greater activity was recorded on the ipsilateral side of the body. At the same time, the vertical components of the hindlimb retractor muscles produce a moment tending to cause pelvic anteversion and thus sagittal flexion (Gray, 1968). To resist sagittal flexion, bilateral activity of the epaxial muscle is necessary. Accordingly our recordings showed a greater level of bilateral symmetry close to the limb girdle at L6.

Similarly, our observation that both epaxial muscles showed two peaks during their main activity at T13, but not at L3 and L6, may be connected to the epaxial muscles stabilizing the trunk against extrinsic forelimb muscle action. The first peak coincides with ipsilateral forelimb touch down, whereas the second peak coincides with the activity at other vertebral levels. The activation of forelimb retractors such as the *m. latissimus dorsi* in walking dogs corresponds in timing with the first peak of the main activity at T13 (Tokuriki, 1973a; Goslow et al., 1981). Because the *m. latissimus dorsi* originates from the dorsal spines and inserts onto the humerus, its activity would not only retract the limb but also tend to laterally bend the trunk (Evans, 1993). To counteract lateral extension and provide a firm base for the forelimb retractor, ipsilateral epaxial muscle activity is expected and was observed for both epaxial muscles. Because this activity was unilateral, a net lateral bending moment results from this first peak. The relatively greater amplitude of the first compared with the second peak in the *m. multifidus lumborum* than in the *m. longissimus thoracis et lumborum* implies that the former functions more as a stabilizer of the vertebral column than the latter, consistent with their topography (Evans, 1993) and fiber type composition (Schilling, 2009).

A similar function of the epaxial musculature in stabilizing the vertebral column against extrinsic muscle action was suggested for salamanders (Barclay, 1946) and experimentally shown for the newt (Delvolve et al., 1997). In terrestrial stepping, the activity of the *m. dorsalis trunci* shows two peaks during the main activity as in dogs. Only the first peak coincided with the activity of the *m. latissimus dorsi*, while the second peak was synchronized with the main bursts of the other trunk segments (Delvolve et al., 1997). A main burst comprising two peaks, of which only the second one corresponded with the main bursts at other vertebral levels, was also observed for the *m. erector spinae* at T7 and T12 but not at T3 or L4 in humans (de Seze et al., 2008). The timing of this first peak, again, coincides with the activity of the ipsilateral *m. latissimus dorsi* functioning during forelimb swinging (Cappellini et al., 2006).

Epaxial muscle function during trotting

Similar to walking, and as discussed in our previous study, the timing and the asymmetry in recruitment are consistent with both epaxial muscles functioning to globally stabilize the trunk against extrinsic hindlimb muscle action and long-axis torsion during trotting (Schilling and Carrier, 2009). In contrast to the previous report, our re-analysis of the trot data shows that the timing of the epaxial muscle activity is also appropriate to produce lateral bending of the trunk. As stated above, to produce lateral bending, muscle activity is expected to occur around lift off of the ipsilateral hindlimb, and this was observed when the dogs trotted.

The comparison between walk and trot revealed several substantial differences in the recruitment of the two epaxial muscles studied. First, all vertebral levels showed a biphasic and bilateral activity, confirming previous results from trotting dogs (Tokuriki, 1973b; Ritter et al., 2001), cats (English, 1980) and horses (Robert et al., 2001; Licka et al., 2004; Wakeling et al., 2007). The greater bilateral symmetry during trotting than during walking suggests a

relatively greater extensor moment at all vertebral levels during trotting, but particularly at T13. Likewise, a greater net extensor moment was observed for the *m. longissimus dorsi* in trotting horses when compared with walking (Wakeling et al., 2007). Consistent with an overall reduced net lateral bending moment, lateral bending decreases when mammals switch from a walk to a trot (Carlson et al., 1979; Pridmore, 1992; Haussler et al., 2001; Robert et al., 2002).

Second, muscle recruitment was significantly higher when the dogs trotted than when they walked (except L6 in the *m. longissimus thoracis et lumborum*). The mid-trunk was the most affected by this increase in activity. Compared with walking, the animal's CoM undergoes greater vertical oscillations during trotting and these oscillations occur during a shorter time period (Tokuriki, 1973a; Tokuriki, 1973b; Cavagna et al., 1977). This results in an overall greater sagittal bending moment that is counteracted by the epaxial musculature (Ritter et al., 2001; Robert et al., 2001). Accordingly, when the dogs switched from a walk to a trot, epaxial muscle activity increased the most at T13, the recording site nearest the CoM. Additionally, compared with walking, greater accelerations and decelerations are required to swing the limbs back and forth during each trotting stride and therefore the locomotor forces acting on the trunk are likely greater during trotting. Our result of an overall increased recruitment of both epaxial muscles during trotting is in accordance with this. Similarly, significant differences in epaxial muscle recruitment between walk and trot were reported for horses (Wakeling et al., 2007; Zaneb et al., 2009).

Recruitment of both epaxial muscles during trotting also differed from that observed during walking in that the main activity exhibited only one peak at T13. When dogs trot at constant speed on level surfaces, the forelimb functions as a strut, i.e. no active protraction and retraction is necessary. The main function of retractors such as the *m. latissimus dorsi* is to brake and inverse the forward motion of the forelimb during the end of swing phase (Carrier et al., 2008). Thus, less stabilization against lateral bending moments due to forelimb retractor muscles may be necessary. Additionally, due to the relatively later touch down of the ipsilateral forelimb, retractor activity occurs relatively later during the stride cycle and thus likely coincides with the main burst.

In contrast to walking, the activation of the epaxial muscles points to a standing wave when dogs trot (Tokuriki, 1973b; Schilling and Carrier, 2009) (this study). In humans, activation of the *m. erector spinae* becomes increasingly synchronized along the back with increasing running speed (Cappellini et al., 2006). In trotting horses, however, lateral bending in the lumbo-sacral joint was out of phase with the bending in the more cranial trunk region (Haussler et al., 2001) and the activity of the *m. longissimus dorsi* showed a cranio-caudal sequence (Licka et al., 2004; Wakeling et al., 2007). The horses, however, showed a longer common ground contact time of the hindlimbs than the dogs investigated in this study [duty factor >0.5 vs <0.5 (Hildebrand, 1966)]. Thus, the observed differences in the activation patterns between dogs and horses may be related to the differences in the timing of the footfalls and therefore in the timing and pattern of trunk bending.

Epaxial muscle function during galloping

In contrast to the symmetrical gaits, both epaxial muscles were active monophasically when the dogs galloped, as has been observed previously for the *m. longissimus* in one dog (Tokuriki, 1974) and the epaxial muscles in cats (English, 1980; Zomlefer et al., 1984). Muscle activity was well synchronized between the respective vertebral levels on both sides of the body. This, together with the timing of the muscle activity, is consistent with the epaxial muscles

functioning first and foremost as extensors and thus as mobilizers of the spine during galloping.

Kinematic analyses have shown that spinal flexions and extensions are synchronized with the cycling of the trailing rather than that of the leading hindlimb (Hildebrand, 1959; Schilling and Hackert, 2006). Consistent with this, epaxial muscle activity in galloping dogs started before the touch down and ended with the lift off of the trailing hindlimb. Furthermore, pelvic retroversion started before the touch down of the trailing hindlimb (Schilling and Hackert, 2006) and, correspondingly, epaxial muscle activity began during the last third of the trailing hindlimb's swing phase in cats (English, 1980) and dogs (this study). In contrast to trotting, the greatest increase in muscle recruitment was observed at L6 when the dogs galloped. Consistent with this, the greatest amplitude of sagittal bending occurs in the presacral joints (Schilling and Hackert, 2006).

In both epaxial muscles, the main activity comprised two peaks. Compared with the main peak, the second peak was more distinct in the *m. longissimus thoracis et lumborum* than in the *m. multifidus lumborum*. In the *m. longissimus thoracis et lumborum*, the second peak was more distinct at T13 and L6 than at L3. The smaller peak at T13 coincided with the end of the ipsilateral forelimb's swing phase. Forelimb retractors such as the *m. latissimus dorsi* are active at the end of swing in galloping dogs (Tokuriki, 1974; Goslow et al., 1981). Because during both trotting and galloping the forelimbs act as struts, forelimb muscle action can be assumed to be similar in the two gaits (Walter and Carrier, 2007), i.e. the *m. latissimus dorsi* functions to break and inverse the limb's forward motion (Carrier et al., 2008). As discussed above, action of the *m. latissimus dorsi* causes lateral extension of the spine, which can be counteracted by ipsilateral epaxial muscle activity. The timing of epaxial muscle activity and the observation that the second peak was relatively greater in the thoracic than in the posterior lumbar site are consistent with the epaxial muscles functioning to globally stabilize the spine.

Further, the peak at the end of the main activity coincided with the end of the swing and the beginning of the stance phase of the leading hindlimb. At this time, hindlimb retractor muscles likely function to actively retract the femur (Schilling et al., 2009) because, similar to trotting, the hindlimbs act as levers during galloping (Walter and Carrier, 2007). The vertical components of the retractor muscle action cause anteversion of the pelvis and thus sagittal flexion (Gray, 1968). Consistent with the function of globally stabilizing the pelvic girdle and counteracting sagittal flexion, bilateral epaxial muscle activity close to the pelvic girdle was observed at this time during the stride. Simultaneously, the horizontal components of retractor muscle action cause lateral extension on the contralateral trunk side (Schilling and Carrier, 2009). In accord with lateral stabilization of the pelvic girdle, epaxial muscle activity was greater contralateral to the leading hindlimb. Additionally, the peak at the end of the main activity occurred at a time during the stride cycle when only the trailing hindlimb was on the ground and thus torsional moments act on the trunk. Consistent with the function of stabilization against long-axis torsion, unilateral activity ipsilateral to the supporting limb was observed.

In galloping mammals, sagittal bending movements follow a cranio-caudal sequence, such that flexion and extension movements in the cranial intervertebral joints precede movements in the caudal joints (Schilling and Hackert, 2006). Consistent with this, muscle activity was recorded at T13 before L3 and at L3 before L6. A cranio-caudal activation pattern was also found in galloping cats, although not discussed [see figure 4 in English (English, 1980)].

Evolution of epaxial muscle function in craniates

Observations on lamprey (Williams et al., 1989), diverse cartilaginous and actinopterygian fishes (e.g. Jayne and Lauder, 1995; Altringham and Ellerby, 1999; Coughlin and Rome, 1999) as well as lungfish (Horner and Jayne, 2008) consistently show a rhythmic, unilateral, alternating and posteriorly propagating activation of the axial muscles during swimming appropriate to produce a traveling wave of trunk motion. Consequently, the ancestral function of the axial musculature during locomotion is to mobilize the trunk (Fig. 4). Similar to fish, when salamanders swim, their axial muscles are activated unilaterally and sequentially (Frolich and Biewener, 1992; D'Aout et al., 1996). During terrestrial locomotion, both kinematic and electromyographic results point to a standing wave of lateral bending, resulting from coordinated epaxial and hypaxial muscle activity (Roos, 1964; Frolich and Biewener, 1992; Carrier, 1993). The main epaxial muscle, active during the second half of ipsilateral hindlimb support and throughout the swing phase (Fig. 4A), was shown to laterally bend the trunk but also to provide postural stability during terrestrial stepping (Deban and Schilling, 2009). Additional activity close to the limb girdles stabilizes the trunk against extrinsic limb muscle action (Delvolve et al., 1997). These observations are consistent with the hypothesis that in addition to the ancestral function as a mobilizer, the evolution of limbs and the transition to land required that the epaxial muscles functioned to globally stabilize the trunk against inertial and extrinsic limb muscle forces as well as gravitational forces (Fig. 4B).

In trotting lizards, synchronized muscle activity along the trunk implies a standing wave of trunk motion (Reilly, 1995; Ritter, 1995; Ritter, 1996). Because activity occurred primarily during ipsilateral hindlimb support and lasted only shortly into swing phase during trotting, Ritter suggested that the epaxials are not involved in lateral bending (Ritter, 1995). Instead, he proposed that they primarily stabilize the trunk against the vertical components of the ground reaction forces and thus against long-axis torsion. Recordings from walking lizards, however, suggest that the activity of the epaxial muscles is appropriate to produce lateral bending (S. Moritz, personal communication) (Fig. 4A). Because of its timing, the unilateral, monophasic activity during hindlimb stance could also stabilize the trunk against the horizontal components of extrinsic limb muscle action and thus restrict lateral bending as shown for salamanders (Delvolve et al., 1997) and dogs (Schilling and Carrier, 2009). Compared with mammals, the horizontal components of extrinsic limb muscle action can be expected to be greater in lizards because of their sprawled limb posture that involves protraction and retraction of the stylopods in more or less the horizontal plane (Brinkman, 1981; Rewcastle, 1981; Jenkins and Goslow, 1983). Because denervation of the epaxial muscles did not influence the lateral bending, Ritter ruled out the function of resisting lateral bending (Ritter, 1995). But the experiment was carried out at the mid-trunk, at which the impact of extrinsic limb muscle action is likely to be small due to muscle topography. Furthermore, possible compensatory action by other axial muscles (e.g. the hypaxial muscles) was not investigated. However, epaxial activity in lizards was similar to that of salamanders in that the muscles were unilaterally active mainly during ipsilateral hindlimb support (Fig. 4A).

In contrast to other tetrapods, mammals display a biphasic and therefore bilateral activity pattern in the *mm. multifidus* et *longissimus* during symmetrical gaits (Tokuriki, 1973a; Tokuriki, 1973b; Carlson et al., 1979; English, 1980; Shapiro and Jungers, 1994). Of these, only the main burst occurring during ipsilateral

hindlimb stance corresponds to the epaxial activity observed in other tetrapods (Fig. 4A). In dogs, this main activity was shown to provide dynamic stability of the trunk against the horizontal components of extrinsic limb muscle activity and long axis torsion (Schilling and Carrier, 2009) and is suggested to also mobilize the trunk; similar to its functions in salamanders and, likely, lizards. The second burst, associated with the second half of ipsilateral hindlimb swing, distinguishes mammals from other tetrapods. The resulting bilateral activity stabilizes the trunk against 'sagittal rebound' due to the inertia of the CoM (Ritter et al., 2001; Robert et al., 2001) and the sagittal components of extrinsic limb muscle action (Schilling and Carrier, 2009). Both components likely have a greater impact on the trunk in mammals than in other tetrapods due to the greater sagittal mobility in the lumbar region and the parasagittal limb posture of mammals. The vertical moments acting on the trunk of a lizard can be assumed to be similar to those acting on the trunk of a mammal with the same body size and locomotor speed, but the vertical displacements of the CoM are likely to be largely passively stabilized in lizards by the horizontal orientation of their zygapophyseal joints. In contrast, in mammals sagittal stabilization requires muscular activity due to their more vertically oriented zygapophyseal facets. Further, due to the parasagittal limb posture of mammals, action of the protractors and retractors of the limbs affects the sagittal plane to a greater extent than the horizontal plane, and thus causes primarily sagittal rather than lateral moments. Because of the greater sagittal mobility of the spine and greater sagittal moments on the spine, the epaxial muscles must play a greater role in dynamic stabilization in the sagittal plane in mammals than in other tetrapods (Fig. 4B).

During the phylogeny of mammals, the increased need for muscular stabilization in the sagittal plane was associated with changes in the architecture of the epaxial muscles. Compared with lizards with their more basal tetrapod trunk morphology, mammals have relatively larger *mm. multifidus* et *longissimus*. Hence, the two epaxials best suited to provide sagittal stability and mobility due to their position relative to the neutral axis of the spine are increased in size in mammals (Slijper, 1946). In contrast, the *m. iliocostalis*, most prominent in lizards and best suited to provide lateral mobilization and stabilization, is reduced in size in mammals (Slijper, 1946). Additionally, the fascicles of the epaxial muscles are primarily parallel to the long-axis of the body in lizards (except the *m. transversospinalis*), whereas those of all epaxial muscles in mammals have a distinct oblique orientation (Nishi, 1916; Slijper, 1946; Tsuihiji, 2005). An oblique orientation allows for mobilization and stabilization in all planes of the body simultaneously and thus better meets the complex needs for trunk mobility and stability in mammals (Fig. 4A). An oblique or roughly pennate architecture is also advantageous to generate greater forces over shorter tendon excursion distances, compared with a longitudinal arrangement, because it allows more fibers to attach to the tendon and decreases the tendon excursion (Brainerd and Azizi, 2005). Hence, the two epaxial muscles with the best leverage to act in the sagittal plane, the *mm. multifidus* et *longissimus*, in particular show morphological and physiological adaptations in mammals to meet the increased need for sagittal mobilization and stabilization.

Both the sequential activation of the epaxial muscles during walking and galloping in mammals and the synchronized activity along the trunk during trotting resemble plesiomorphic activation patterns shared with other vertebrates. Sequential activation is ancestral for the axial musculature of all vertebrates, while synchronized axial activity may have evolved during the evolution of tetrapods (Ijspeert et al., 2007) or, more likely, derived from the

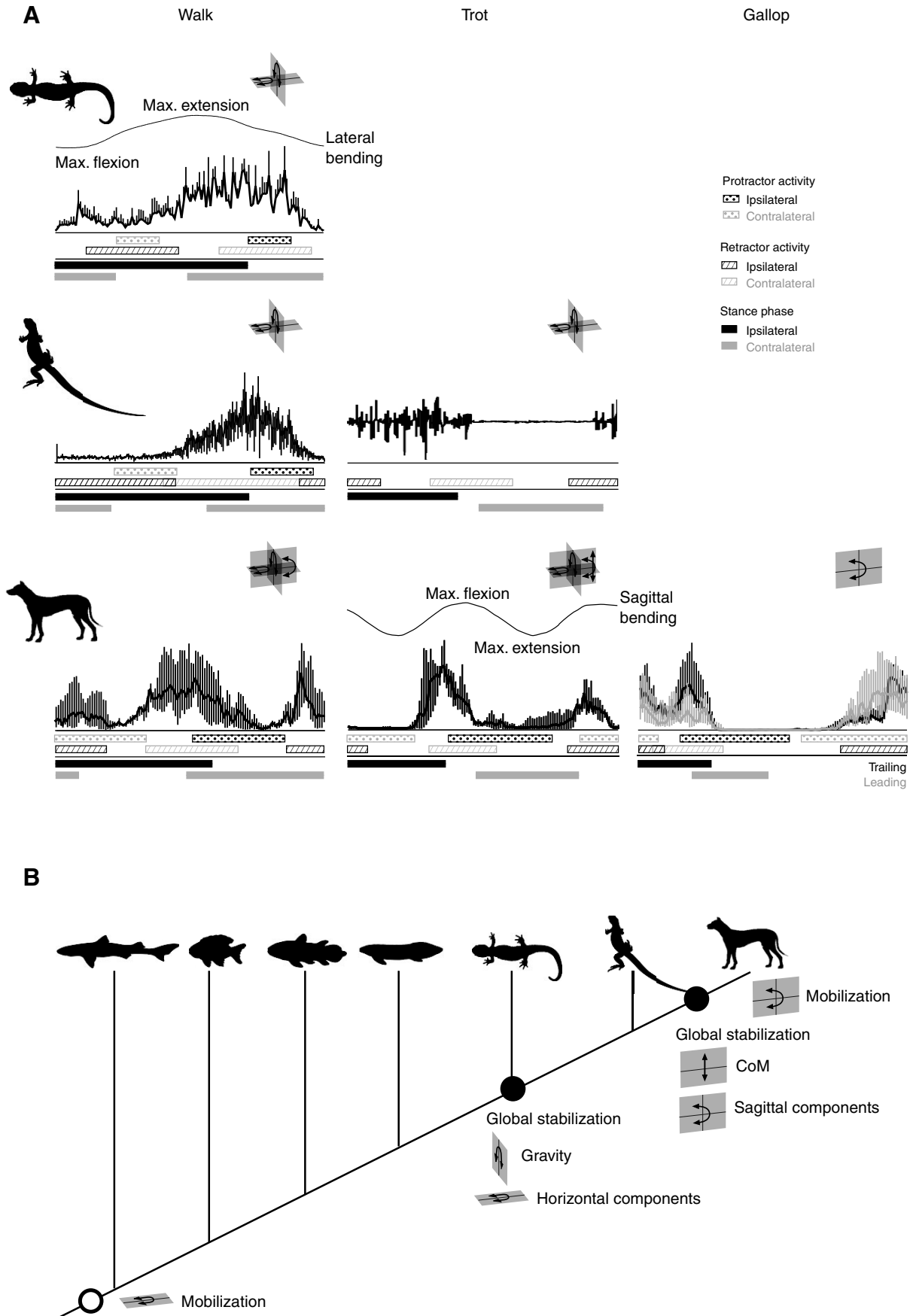


Fig. 4. For legend see next page.

Fig. 4. (A) Timing of the activity and hypothesized functions of the epaxial muscles in tetrapods during locomotion. Data for epaxial muscle activity are assembled from: salamander, *Ambystoma maculatum*, m. dorsalis trunci, mid-trunk (Deban and Schilling, 2009); walking lizard, *Dipsosaurus dorsalis*, m. longissimus dorsi, mid-trunk (S. Moritz, unpublished data); trotting lizard, *Varanus salvator*, m. longissimus dorsi, mid-trunk (Ritter, 1995); mammal, *Canis familiaris*, m. longissimus thoracis et lumborum, posterior trunk (this study). The x-axis represents the stride cycle beginning with touch down of the ipsilateral hindlimb. The footfall patterns of both hindlimbs are illustrated on the bottom of each graph (solid bars). Additionally, the timing of the activity of hindlimb protractors (dotted bars) and retractors (hatched bars) is plotted to illustrate the activity phase relationships of the epaxial and extrinsic limb muscles. Protractor activity data: salamander, *Dicamptodon tenebrosus*, m. puboischiofemoralis internus (Ashley-Ross, 1995); walking alligator, *Alligator mississippiensis*, m. puboischiofemoralis internus (Reilly and Blob, 2003); mammal, *Canis familiaris*, m. sartorius (Schilling et al., 2009) (N.S., S. M. Deban and D.R.C., unpublished data). Retractor activity data: salamander, *Dicamptodon tenebrosus*, m. caudofemoralis (Ashley-Ross, 1995); lizard, *Dipsosaurus dorsalis*, m. caudofemoralis (Nelson and Jayne, 2001); mammal, *Canis familiaris*, m. semimembranosus (Schilling et al., 2009) (N.S., S. M. Deban and D.R.C., unpublished data). For the salamander and the trotting dog, bending traces above the EMGs illustrate the unimodal lateral and the bimodal sagittal bending of the trunk during the course of a stride (from Deban and Schilling, 2009; Ritter et al., 2001). Body planes in which moments and/or movements are suggested to occur are illustrated in the right top corner of each graph (for details see B). Note that the unilateral and monophasic epaxial activity in salamanders and lizards associated with the ipsilateral stance phase corresponds to the main activity observed in mammals. In mammals, the increased need for sagittal stability is met by bilateral activity resulting from a second activity during ipsilateral swing phase. (B) Suggested epaxial muscle functions mapped onto a simplified phylogenetic hypothesis of gnathostomes to illustrate the evolutionary changes in epaxial muscle function during the phylogeny of tetrapods. The plesiomorphic function to mobilize the trunk in the horizontal plane is represented by an open circle. Connected with the evolution of limbs and the transition to land, the epaxial muscles additionally function to globally stabilize the trunk against inertial and extrinsic limb muscle forces as well as against gravitational forces. Note that the extrinsic muscle forces occur primarily in the horizontal plane due to the sprawled limb posture. Associated with the evolution of sagittal mobility in the spine and a parasagittal limb posture, the epaxial muscles of mammals additionally function to globally stabilize the trunk against the sagittal components of the extrinsic limb muscles as well as the inertia of the center of body mass (CoM) during symmetrical gaits. During asymmetrical gaits, the epaxial muscles primarily function to mobilize the trunk in the sagittal plane.

motor pattern of C-start behavior as described for fish (Hale, 2002). However, our results support the hypothesis of a phylogenetic conservatism of the spinal locomotor networks generating axial motor patterns (Chevallier et al., 2008). Endorsed by kinematic results (Ashley-Ross and Bechtel, 2004) and based on their spinal cord model, that spontaneously produces traveling waves but standing waves only when limb oscillatory centers are implemented, Ijspeert and colleagues suggested that traveling waves of the body do not concur with limb movements (Ijspeert et al., 2007). Thus, our observation of a traveling wave during walking and galloping contradicts these numerical data of fictive locomotion that question the co-existence of traveling waves of body motion with limb movements (Ijspeert et al., 2007).

Compared with anamniotes, the sequential activation patterns of the epaxial muscles are less evident in mammals. The patterns can be expected to be obscured in mammals due to the evolution of polysegmental muscle tracts and thus the loss of the ancestral segmentation of the axial musculature (Starck, 1978). Additionally, perhaps connected to the increased need for sagittal stability, waves of muscle recruitment producing and/or restricting lateral and/or

sagittal bending may propagate in opposite directions. For example, lateral bending was shown to travel in the cranio-caudal direction, while sagittal bending traveled in the caudo-cranial direction in horses (Haussler et al., 2001). Further, sequential and synchronized recruitment may interfere with each other. For instance, during walking, lateral bending travels along the trunk associated with a sequential activation, while simultaneously trunk stabilization against long-axis torsion likely requires a more synchronized activity throughout the trunk. Nevertheless, the underlying recruitment patterns in mammals resemble the ancestral patterns of vertebrates, despite profound changes in the topography and additional functions of the epaxial musculature in mammals.

CONCLUSIONS

The axial musculoskeletal system is one of the most complex systems in the mammalian body because of its multiple functions and various degrees of freedom. Depending on the gait and the particular moments acting on the spine during a locomotor cycle, both epaxial muscles studied here are suggested to cause and/or counteract moments in the horizontal, the transverse and/or the sagittal planes. Thus, they are hypothesized to produce motions of the trunk as well as to stabilize it against gravitational and inertial forces of the trunk and limbs and forces produced by extrinsic limb muscles. Further, epaxial muscle function appears to depend on the vertebral level, as indicated by differences in timing and activation along the trunk. These cranio-caudal differences in muscle recruitment together with morphological differences within the muscles allow for segmental variation and adaptation of epaxial muscle function along the trunk and appropriate responses to locomotor events. Indeed, the function of a given epaxial muscle such as the m. multifidus varies along its length even during the course of a single stride. Consequently, the anatomical unit 'muscle' cannot be considered as one, homogeneous functional unit in the axial system.

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