Epaxial muscle function in trotting dogs

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Summary

One of the features that distinguish mammals from other groups of terrestrial vertebrates is the structure and relative size of their epaxial muscles. Yet we have only a superficial understanding of the role these muscles play in locomotion. To address their locomotor function, we recorded the electrical activity of the iliocostalis, longissimus dorsi and multifidus muscles of trotting dogs. Activity was monitored at both lumbar and thoracic sites. To develop and evaluate hypotheses of epaxial muscle function, we quantified footfall patterns and sagittal trunk kinematics from high-speed videos, and the magnitude and orientation of ground reaction forces from force-plate recordings. All three epaxial muscles tended to exhibit a double-bursting (biphasic) activity pattern, with the exception of the iliocostalis muscle at the thoracic site (which was uniphasic). In general, a large burst of activity in each muscle occurred during the second half of the support phase of the ipsilateral hindlimb, and was active for an average of 30 % of the locomotor cycle. A smaller burst of activity occurred during the second half of the support phase of the contralateral hindlimb, and was active for an average of 15 % of the locomotor cycle. Analysis of ground reaction forces and sagittal trunk kinematics led us to the hypothesis that the epaxial muscles do not directly stabilize the trunk against the vertical and horizontal components of the ground reaction force. Instead, the epaxial muscles appear to counteract the tendency of the trunk to rebound (flex) in the sagittal plane during the latter half of the support phase. This hypothesis of epaxial muscle function was supported by loading experiments performed on the longissimus dorsi muscle in the lumbar region.

Key words: epaxial muscle, electromyography, locomotion, dog, trotting.

Introduction

"*With the appearance of mammals and their subsequent development to a major position in the vertebrate world, proficiency in land locomotion reached its zenith.*" Rockwell et al., 1938, p. 101.

Mammals, especially those described as cursors, are believed to possess an adaptive locomotor complex that includes parasagittal limb orientation and associated movement of the trunk in the sagittal plane (Rockwell et al., 1938; Gray, 1968; Rewcastle, 1981). The selective advantages attributed to this configuration include increased speed, endurance, acceleration and maneuverability; all factors that are presumably important in ecologically relevant activities such as migration, intraspecific competition and predator-prey interactions (Hildebrand, 1995). The epaxial muscles of mammals form an integral part of this locomotor complex. For example, the role of the epaxial muscles in producing sagittal movements of the body axis is a critical component of galloping, a high-speed gait that is only observed in mammals (with the notable exception of some crocodilians). These sagittal movements, in addition to coordinating limb movements, are estimated to increase the top speed of a sprinting cheetah by 6 miles per hour (Hildebrand, 1961).

Several studies have addressed the locomotor function of the epaxial muscles during walking and trotting in mammals. These studies have focused on a single site on the trunk (lumbar site of cats: English, 1980; Carlson et al., 1979), only one of the epaxial muscles (longissimus dorsi muscle: Tokuriki, 1974), or on animals that do not exhibit a typical quadrupedal gait (e.g. primates: Thorstensson et al., 1982; Carlson et al., 1988; Shapiro and Jungers, 1988; Shapiro and Jungers, 1994). In all cases, these studies have concluded that the epaxial muscles 'support' or 'stabilize' the trunk during walking and trotting. Not surprisingly, the specific aspect(s) of the locomotor forces against which the epaxial muscles stabilize the trunk, has not been elucidated. A muscle that 'stabilizes' the body (i.e. a postural muscle) will, by definition, resist movement. Resistance of movement, if successful, will result in a lack of movement. Therefore the specific function(s)

of a stabilizing or postural muscle is very difficult to see, and even more difficult to test.

This study combines a thorough description of the activity of the epaxial muscles in trotting dogs with an attempt at a more detailed functional analysis of these muscles. Trotting was studied because it appears to be the basal running gait for terrestrial vertebrates. It is present in salamanders, lizards and mammals, and therefore provides a means of comparison among tetrapods that should facilitate our understanding of the evolution of both terrestrial locomotion and of epaxial muscle function in vertebrates.

Materials and methods

Dogs

Data from ten dogs (seven female, three male) of mixed breeds are reported here. All were medium-sized dogs, with a mean body mass of 21.5±1.7 kg. Six were purchased at approximately 1 year of age from a USDA-licensed animal dealer. Four were obtained from animal shelters in Utah. All dogs were adopted as pets at the conclusion of their experimental careers. Dogs were chosen as experimental animals for several reasons. First, they are willing and able subjects that appear to be thoroughly comfortable on the treadmill. Their willingness and comfort on the treadmill increases our confidence in the data obtained from them. Second, dogs may be described as typical cursorial mammals. If there is a functional differentiation of the epaxial muscles that is involved with upright limb posture and limb movements in a sagittal plane, it should be obvious in a cursor such as a dog. Third, dogs exhibit all three of the typical mammalian gaits: walking, trotting and galloping.

Muscular anatomy

We verified the anatomy of the epaxial muscles through dissection of cadavers. A brief description of the epaxial muscles (condensed from Evans, 1993) is given below.

The most medial epaxial muscle we recorded from was the multifidus, one of the transversospinalis muscle group. The multifidus is a segmental muscle, the individual segments of which originate from the articular, transverse or mammillary process of a vertebra, generally span two vertebrae, and insert on the spinous process of a cranial vertebra. There are four portions of the multifidus, named according to the region of the trunk they are associated with. We implanted electrodes in the multifidus lumborum and the multifidus thoracis.

Lateral to the multifidus is the longissimus dorsi muscle, the most robust of the epaxial muscles. The longissimus dorsi is composed of overlapping muscle fascicles of variable length that extend from the iliac crest to the skull. The longissimus dorsi is divided into the thoracolumbar, cervical and capital regions. The thoracolumbar region may be further divided into a longissimus lumborum and a longissimus thoracis, and these are the two regions we recorded from. Fascicles of the longissimus lumborum originate from the ileum and insert on the accessory processes of the first to sixth lumbar vertebrae.

Fascicles of the longissimus thoracis also originate from the ileum, and end in bifurcating tendons that attach to the caudal borders of the sixth to thirteenth ribs, and the accessory processes of the sixth to thirteenth thoracic vertebrae.

The most lateral of the epaxial muscles is the iliocostalis, which also consists of multiple fascicles and may be divided into a lumbar and thoracic region. The iliocostalis lumborum arises from the ileum, and consists of fascicles that attach to the tenth through the thirteenth ribs. Fascicles of the iliocostalis thoracis arise from the cranial aspect of the vertebral ends of the ribs. The fascicles form a common belly, and from this muscle belly tendons arise which insert on the caudal aspects of the ribs and on the transverse process of the seventh cervical vertebra.

Electromyography

Electrical activity of the epaxial muscles was recorded from two dogs trotting on a motorized treadmill, and from two dogs trotting on a stationary trackway. Each dog underwent two surgical implantations of 12–16 EMG electrodes. Two epaxial sites on the trunk were implanted with electrodes. The lumbar site was approximately mid-way between the crest of the ilium and the last rib, at the level of the fourth lumbar vertebra. The thoracic site was at approximately the level of the sixth thoracic vertebra. Recording of muscle activity began on the second day after surgery and continued for 2–5 days. 5–8 days after implantation the electrodes were removed. The dogs recovered for at least 30 days before the second electrode implantation. All procedures conformed to the guidelines of the Institutional Animal Care and Use Committees at Brown University and the University of Utah.

For surgery, subjects were initially anesthetized with an intravenous injection of Pentethal or Propofol, to effect. They were intubated with an endotracheal tube and maintained on a ventilator with oxygen to 1.3 minimum alveolar concentration and 1.5–2.0 % Isoflurane for the duration of the surgery. Incisions were made through the skin above the site of electrode placement and patch (Loeb and Gans, 1986), or sew-through (Betts et al., 1976) electrodes were secured to the muscles of interest. Lead wires from the electrodes were passed subcutaneously to a dorsal exit point just caudal to the dorsal tips of the scapulae. Electromyographic signals were passed through shielded, light-weight cables (Cooner Wire, Inc.), filtered above 1000 Hz and below 100 Hz, and amplified 5,000 or 10,000 times with Grass P511 AC amplifiers. Data were stored in digital form at 2000 Hz on a PC or Macintosh computer.

Patch electrodes were constructed from 0.3 mm, multistranded, Teflon-insulated stainless steel wire (Cooner Wire Inc.) sewn through 1 cm × 2 cm rectangles of 0.8 mm Silastic sheeting (Dow Corning). The exposed portions of the wires were parallel to one another, approximately 1 mm in length, separated by 1–2 mm, and oriented at 90 ° to the fiber direction of the muscle. Sew-through electrodes were constructed from the same wire as the patch electrodes. An

overhand knot was tied in one end of the two leads. A 1–2 mm length of the insulation was removed from one side of each wire. These uninsulated segments were staggered approximately 6 mm and 8 mm from the knot. A small square (3 mm × 3 mm) of Silastic sheeting was threaded past the exposed portion of the wires to abut the knot. The two lead wires were sewn directly into the muscle, parallel to the muscle fibers, so that the exposed segments of the wires were inside the muscle and the Silastic button acted as a stop. A second Silastic button was then threaded to the point where the wires exited the muscle and secured in place with a square knot in the leads. This provided a secure anchoring of the electrode and the 1–2 mm staggering of the exposed segments parallel to the fiber orientation resulted in a dipole when the muscle was active.

The general pattern of muscle activity was determined by averaging (Banzett et al., 1992; Carrier, 1996) of the electromyographic signals (Fig. 1). For the data from the two dogs running on the treadmill, the beginning and end times of individual cycles were determined from accelerometer signals (an analog signal of the locomotor cycle was obtained from the two treadmill dogs by monitoring the vertical acceleration of the trunk with an Omega 103 accelerometer, mounted dorsally in the lumbar region). These times were used to divide the electromyographic signals into locomotor cycle segments. The electromyographic segments were then rectified, partitioned into 100 bins of equal duration, and a measure of EMG intensity was calculated for each bin by multiplying the number of spikes by the average amplitude of the spikes (EMG 'energy' of Gans and Gorniak, 1980). The EMG activity was then averaged on a bin by bin basis for 20 consecutive locomotor cycles. The resulting trace represents the average EMG activity during an average locomotor cycle. For the data from the two dogs that ran on the stationary track, the beginning and end times of individual cycles were determined using footfalls, taken from videotapes. Because these animals were only in view of the camera for one or two locomotor cycles, single cycles from multiple trials were averaged to produce the mean EMG activity traces.

Kinematics

Locomotor events (footfall events and sagittal movements of the trunk) were recorded on video at 120 Hz with a PEAK high-speed camera. Footfall patterns were quantified in all dogs using frame-by-frame analysis of the video tapes. Sagittal kinematics of the trunk were quantified in three dogs trotting on the treadmill by digitizing three small reflective spheres that were glued to the dorsal midline after shaving

the skin. One marker was placed mid-trunk, at the level of the 11th thoracic vertebrae, and the other two markers were positioned directly over the pectoral and pelvic girdles. The video recordings were synchronized with the EMG and accelerometer recordings with a circuit that simultaneously illuminated an LED in the view of the video camera and triggered data acquisition by the computer.

Force-plate recordings

Single limb ground forces were measured in the two dogs that ran on the trackway. The trackway was carpeted, 35 m long, and had a force plate (Kistler, 9281B SN) located mid-track that was mounted flush with the track floor. The resultant of the single limb ground reaction forces, from sample trials, was combined with video recordings of the same trials to visualize the ground reaction force vectors relative to the trunk and girdles. Fore- and hindlimb force data were combined to produce an average force profile for the support phase of the trot. Recordings from 20 strides were used to generate average ground forces for each dog.
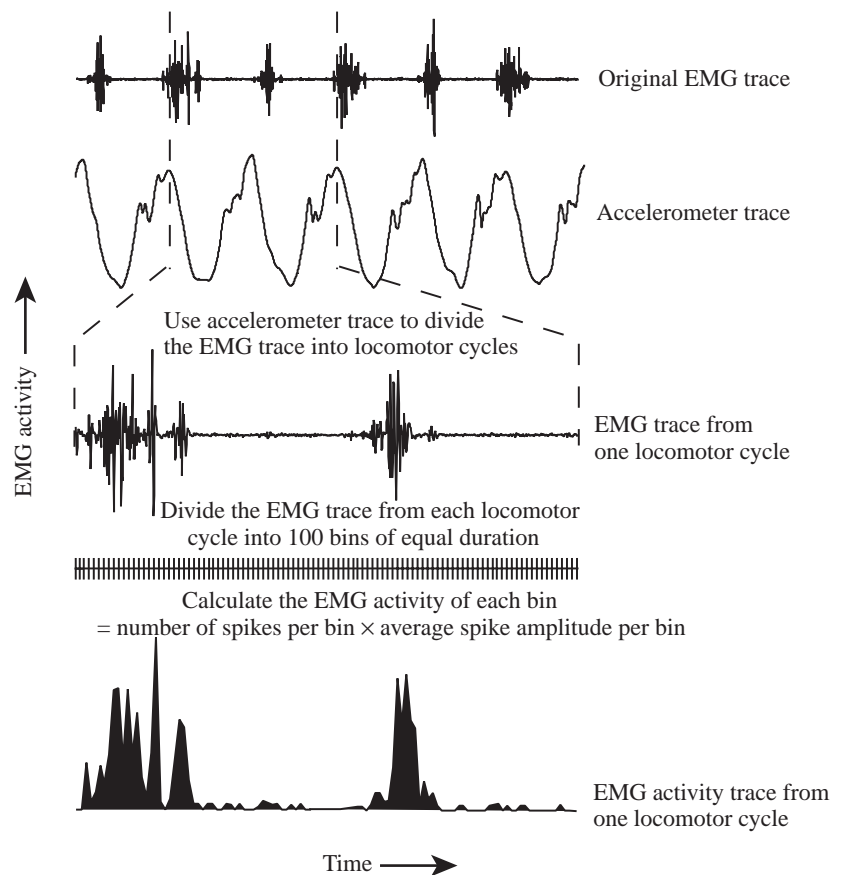

Fig. 1. A summary of the methods used to produce EMG activity traces from treadmill data. An accelerometer trace was used to divide each EMG trace into smaller traces that corresponded to a single locomotor cycle. This trace was then rectified, divided into 100 bins of equal duration, and the EMG activity of each bin was calculated by multiplying the number of spikes in each bin by the mean spike amplitude of each bin. EMG activity traces were then averaged on a bin-by-bin basis to produce a mean EMG activity trace for each muscle at each site.

Loading experiments

To test an emergent functional hypothesis (described below) for the activity of the epaxial muscles during trotting, we conducted experiments in four dogs in which the trunk of the dog was loaded with 8–15 % of body mass. The dogs carried the added mass in saddlebags on their backs in two different configurations. In one case, all of the added mass was carried mid-trunk at the level of 11th thoracic vertebrae. In the other configuration, half the added mass was carried over the pectoral girdle and the other half was carried over the pelvic girdle. Activity of the longissimus dorsi muscle was recorded from each of these dogs as they trotted on the treadmill in three conditions; without the mass, with the added mass positioned over the girdles, and with the added mass positioned over the center of the trunk. EMG signals were filtered above 1000 Hz and below 100 Hz, sampled at 4000 Hz, and stored on a Macintosh computer. The effect of the two manipulations was evaluated by calculating the mean EMG activity (integrated area of the rectified signal) from 20 locomotor cycles from each condition. For each dog, unpaired t-tests were performed to compare the mean EMG activity from the unloaded, girdle-loaded and mid-trunk loaded conditions.

The hypothesis tested by this experiment was that the epaxial muscles function during trotting to resist the tendency for the trunk to rebound (flex) vertically during the second half of limb support (described below). The mid-trunk weight increased the gravitational bending moment on the trunk, and therefore should also increase the rebound of the trunk. If this was true, the mid-trunk loading manipulation would be expected to require greater muscle activity from the muscles that stabilize the trunk against the rebound. The girdle weights should not have increased the gravitational bending moment of the trunk.

Because the hypothesis is one of postural control we do not have a prediction of the extent to which amplitude of flexion would be influenced by the added mass. If we were to observe no change in trunk flexion, but an increase in epaxial activity with the mid-trunk load, we would argue that the epaxial muscles increased activity to effectively control the increased tendency for rebound. Similarly, if we were to observe an increase in trunk flexion and an increase in epaxial muscle activity, we would conclude that the epaxial muscles acted to control the rebound, but were unable to fully correct for the added mass. Stated another way, if the amplitude and velocity of the rebound remained exactly the same in the mid-trunk manipulation, the postural muscles would still be required to exert greater force because the momentum of the mid-trunk would be greater due to the added mass. Hence, we did not monitor the amplitude of trunk flexion and extension in this experiment.

Results

Electromyographic pattern

The EMG data reported here are all from dogs trotting at their self-selected trotting speed, which ranged from 1.5 to 3.0 m s^{-1}. Over this range of speeds we did see variation in the pattern of muscle activity among dogs. However, there was a general pattern of activity for each muscle at each site, which is described below. Variability between animals is addressed after the general description of each muscle's activity. Most muscles exhibited a biphasic activity pattern, and typically one of these bursts was of greater intensity (greater duration and/or amplitude) than the other. The larger burst is referred to as the primary burst, and the smaller burst is referred to as the secondary burst. EMG activity of each muscle is described relative to the footfall pattern obtained from videotape.

Multifidus

The multifidus muscle was very consistent in exhibiting two bursts of activity per locomotor cycle (biphasic activity), with each burst occurring during the second half of the support phase of a pair of limbs (Fig. 2, Fig. 3). Intensity differences between primary and secondary bursts were especially apparent at the lumbar site (Fig. 3). At the lumbar site the primary burst occurred during the second half of the support phase of the ipsilateral hindlimb, and the duration of activity averaged 33 % of one locomotor cycle. The secondary burst occurred during the second half of the support phase of the contralateral hind limb, and was of shorter duration than the primary burst (averaged 18 % of one locomotor cycle). The pattern was very similar at the thoracic site, though the primary burst duration averaged 27 % of cycle duration, while the secondary burst averaged 18 %. At both sites, the midpoint of activity of the secondary burst occurred approximately 50 % of cycle time after the midpoint of activity of the primary burst. This means that there is a period of bilateral activity (overlapping activity of left and right side muscles) during the second half of the support phase of each diagonal pair of limbs, and a period of no EMG activity during the first half of the support phase of each diagonal pair of limbs. This was a very repeatable pattern of activity, regardless of the individual dog recorded from.

Longissimus dorsi

The longissimus dorsi muscle typically exhibited biphasic activity at both lumbar and thoracic sites (Fig. 2, Fig. 3). The activity pattern was similar to that of the multifidus muscle; a primary burst of activity associated with the second half of ipsilateral hindlimb support, and a secondary burst associated with the second half of contralateral hindlimb support. Burst durations at the lumbar site averaged 30 % and 11 % of cycle duration for the primary and secondary bursts, respectively. Burst durations at the thoracic site averaged 30 % and 15 % of cycle duration for the primary and secondary bursts, respectively. The midpoint of activity of the secondary burst occurred approximately 50 % of cycle duration after the midpoint of activity of the primary burst. Therefore, as with the multifidus, there is a period of bilateral activity of the longissimus dorsi muscle, with the secondary burst of activity occurring contralateral to hindlimb support and in the middle of the primary burst that occurs ipsilateral to hindlimb support.
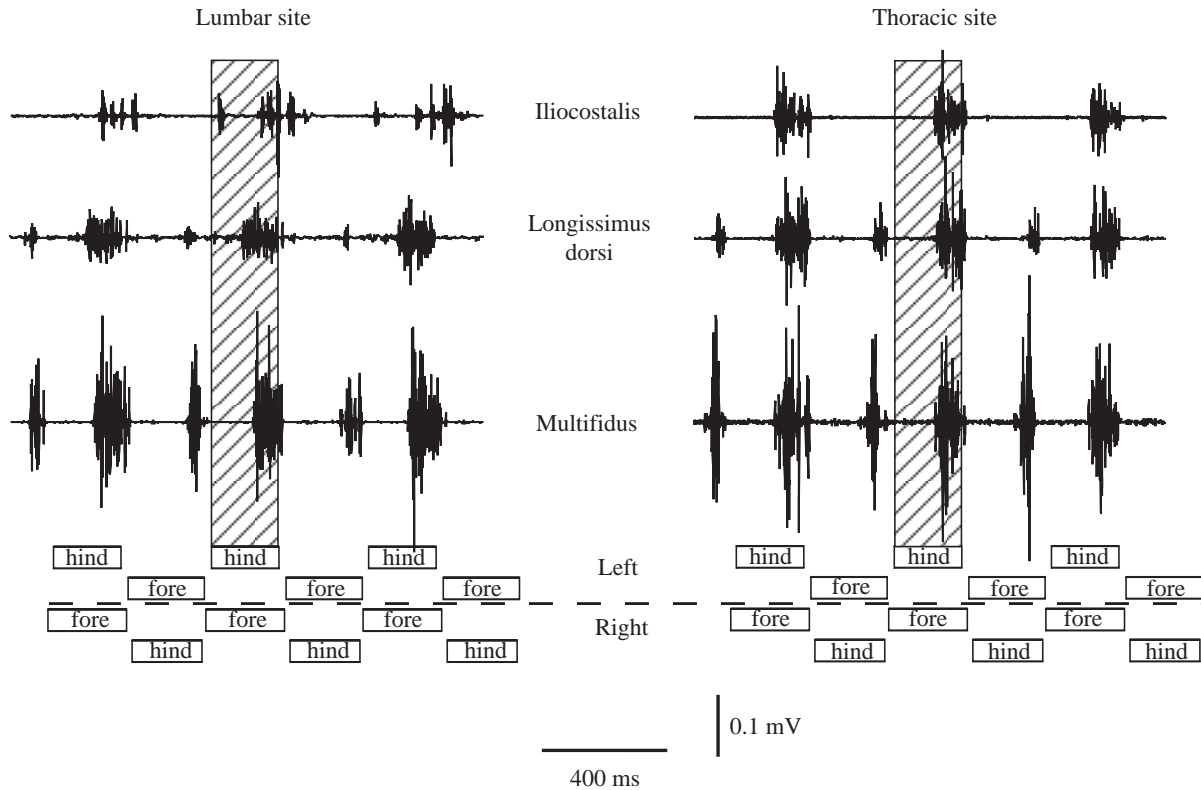
Fig. 2. Raw EMG data from a dog trotting on the treadmill at 2.5 m s⁻¹. All EMG data are from muscles on the animals left side. Footfall diagrams are shown below the EMG traces, with rectangles indicating periods of support by the indicated foot. The cross-hatched rectangles highlight the temporal relationship between muscle activity and ipsilateral rear foot support.

The presence of the secondary burst was variable, and appeared to be related to the speed of the dog. At the lowest trotting speed recorded (1.5 m s⁻¹), activity in the lumbar site was uniphasic, with only the primary burst of activity present. At trotting speeds greater than 1.5 m s⁻¹ (2.0, 2.5 and 3.0 m s⁻¹), the secondary burst of activity was typically present. Two of the four dogs used for the loading experiments showed secondary bursts only when they were carrying added mass.

Iliocostalis

Activity of the iliocostalis muscle was grossly different from both the multifidus and longissimus dorsi activity patterns (Fig. 2, Fig. 3). The thoracic site showed a consistent uniphasic pattern. This activity occupied approximately the second half of the ipsilateral hindlimb support phase, and averaged 30 % of cycle duration. The lumbar site exhibited a biphasic pattern. The primary burst duration averaged 30 % of cycle duration and occurred during the second half of ipsilateral hindlimb support. Although the secondary burst was consistently present at the lumbar site, it was of especially short duration, averaging only 6 % of cycle duration. In one of the dogs (Fig. 3A), the midpoint of activity of the secondary burst occurred 65 % of cycle duration after the midpoint of activity of the primary burst. This means that in that dog in the lumbar region there was no period of bilateral activity of the iliocostalis muscle. A primary burst of activity

ipsilateral to hindlimb support was immediately followed by a secondary burst of activity contralateral to that hindlimb, but the primary and secondary bursts of opposite sides did not overlap. In the other dogs, however, the midpoint of the secondary burst occurred 50 % of the cycle duration after the midpoint of the primary burst, meaning that in these dogs there is a period of overlapping activity of the iliocostalis muscle in the lumbar region.

Ground reaction forces and vectors

Both dogs showed a very regular pattern of ground reaction forces. A combined front/rear mean force trace is first described relative to limb support (Fig. 4). The vertical component of the ground forces exhibited a regular increase during the stance phase of a given pair of limbs, peaked slightly before mid-stance, and then showed a regular decrease towards zero during the second half of the stance phase. The fore–aft component of the ground forces was divided into a deceleration and an acceleration phase. Deceleration occurred during the first part of the stance phase. There was a regular increase in force that peaked at approximately 20 % of the stance phase, then decreased back to zero. At approximately the time of peak vertical force the fore–aft force became positive (becomes an acceleration), peaked at approximately 70 % of the stance phase, and then decreased back to zero. The third component of the ground forces is the lateral force,
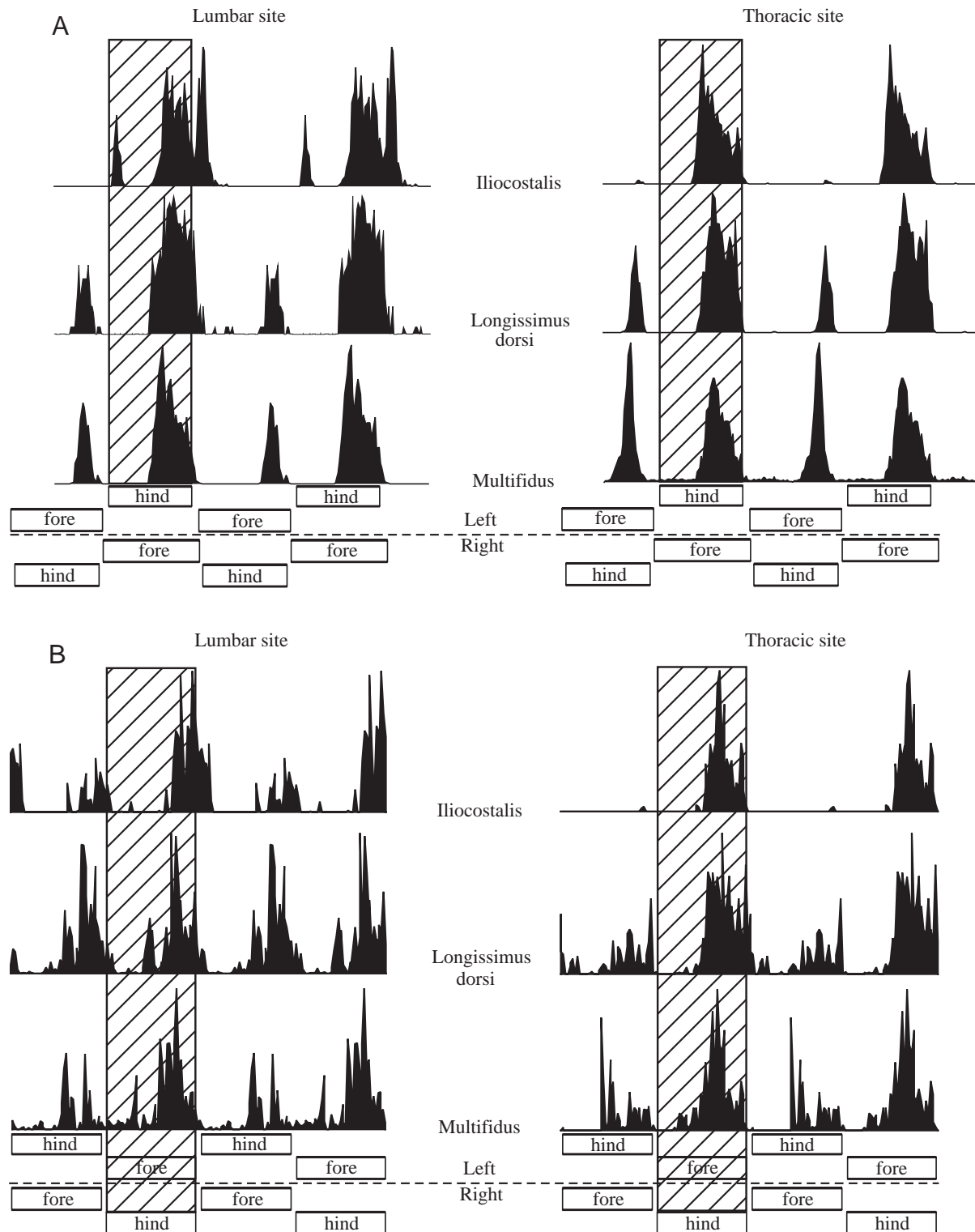
Fig. 3. Mean EMG activity traces from two trotting dogs, one from the treadmill and one from the trackway. In both cases, mean activity data for a single locomotor cycle are repeated so that the general pattern may be more easily seen. (A) Mean EMG activity traces calculated from 20 consecutive cycles of locomotion from a dog trotting on the treadmill at $2.5\,\mathrm{m\,s^{-1}}$. All EMG data are from muscles on the animal's left side. Mean footfall diagrams are shown below the EMG energy traces, with rectangles indicating periods of support by the indicated foot. The cross-hatched boxes highlight the temporal relationship between muscle activity and ipsilateral rear foot support. (B) Mean EMG activity traces calculated from 15 locomotor cycles from a dog trotting along a trackway at a speed of $2.0\,\mathrm{m\,s^{-1}}$. All EMG data are from muscles on the animal's right side. Mean footfall diagrams are shown below the EMG activity traces, with rectangles indicating periods of support by the indicated foot. The cross-hatched boxes highlight the temporal relationship between muscle activity and ipsilateral rear foot support.
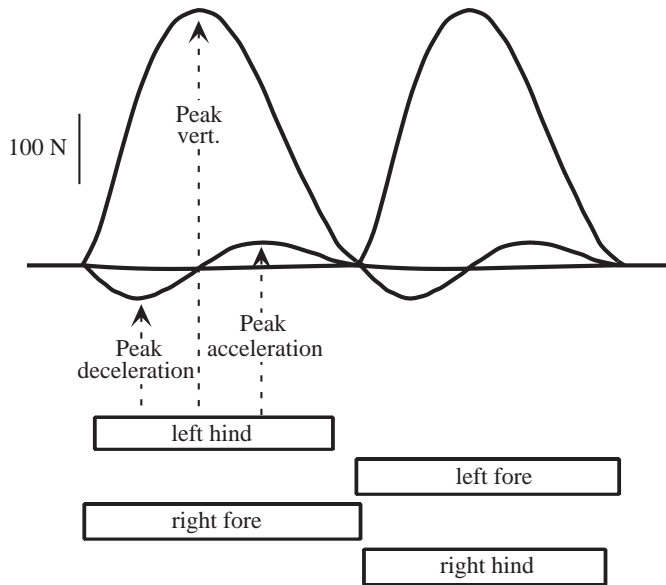
Fig. 4. Mean ground reaction force data for a trotting dog. Data from one step are repeated so that the general pattern may be more easily seen. These data represent the resultant force trace of both limbs, as opposed to single-limb forces, and are averaged from 15 trials of force-plate data. The trace of the large single peak during a step is the vertical (vert.) force. The trace that first drops below and then rises above baseline is the recording of the fore–aft force. The very flat, unlabeled trace is the recording of the lateral force. The average speed of this animal trotting across the force plate was 2.0 m s^{-1}.

which was very small in our recordings and is not considered in this study.

There was a very consistent pattern of epaxial muscle activity relative to the ground forces (Fig. 5). In all muscles, at both the lumbar and thoracic sites, the primary burst of activity began just after peak vertical force, and the muscles were active throughout the acceleratory phase of fore–aft force production. The secondary burst of activity, when present, was also associated with the second half of limb support.

During the initial phase of limb support, the ground force reaction vectors of both fore- and hindlimbs passed just rostral to their respective girdles (Fig. 6). The magnitude of both vectors increased until they peaked approximately halfway through the support phase (Fig. 6, 50 %). At this time, the hindlimb reaction vector was shifted caudally such that it passed through the iliosacral joint. The forelimb vector
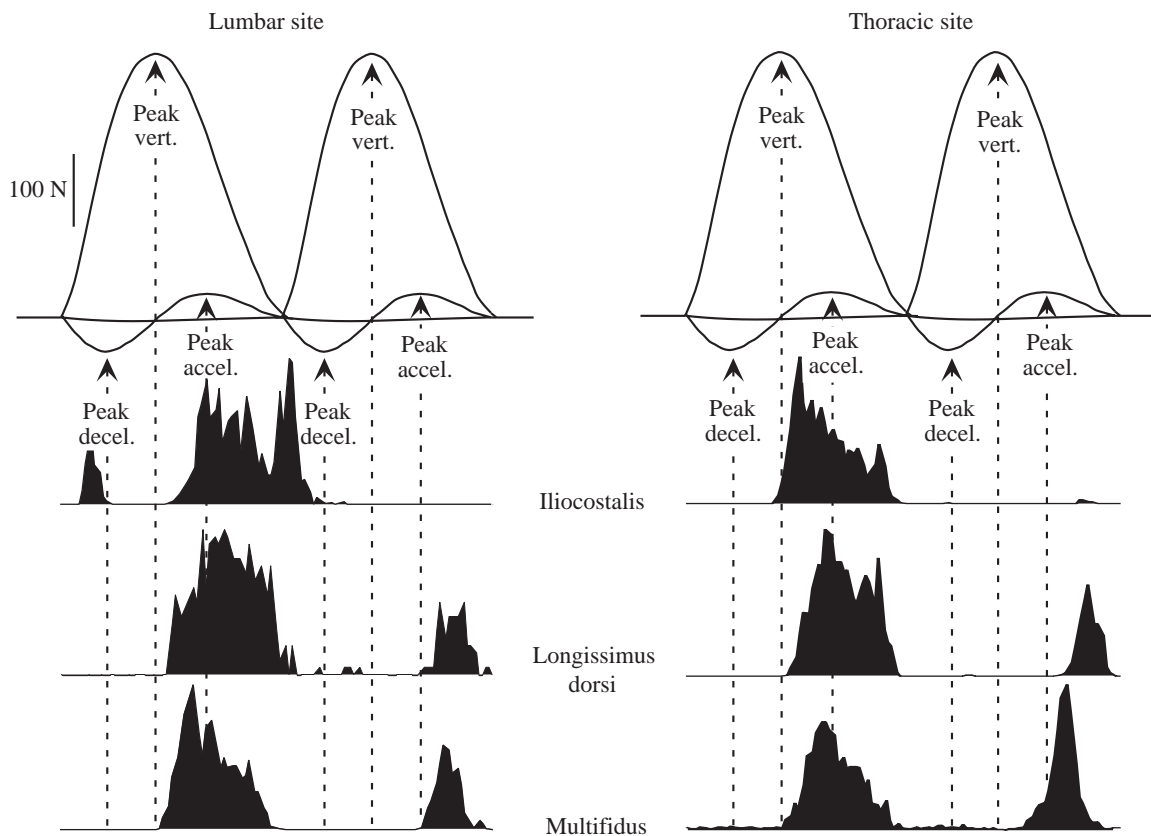

Fig. 5. Ground forces relative to epaxial EMG activity, produced by combining the mean force trace with mean EMG activity traces. The primary burst of epaxial muscle activity begins just after peak vertical (vert.) force, activity occurs throughout the acceleration (accel.) phase of fore–aft force production, and activity ceases at approximately the same time that vertical and horizontal forces return to zero. The secondary bursts are shorter in duration, such that they generally correspond to the second half of the acceleration phase of fore–aft force production. decel., deceleration.

remained just rostral to the shoulder. As the support phase progressed the magnitude of the vectors decreased, and both continued to shift caudally, such that at 75 % of the support phase the hindlimb vector passed just caudal to the iliosacral joint and the forelimb vector passed through the shoulder.

Dorso–ventral kinematics of the trunk

The region of the back between the two limb girdles moved as a unit, such that the entire back underwent a regular cycle of flexion and extension as the animal ran. As a pair of diagonal limbs came into contact with the ground, the back had reached maximum flexion and had begun to extend (Fig. 7). Extension continued until approximately 40 % of the support phase of the step, at which time maximum extension occurred and sagittal movements of the back reversed direction and flexion began. Flexion continued until approximately 93 % of the support phase of the step, at which time maximum flexion occurred. At 100 % of the step cycle the opposite pair of diagonal limbs made contact with the substrate, and the cycle of sagittal bending of the trunk began again. These data show that sagittal flexion and extension occupied approximately equal proportions of the locomotor cycle.

Loading experiments

The loading experiment produced clear differences. A sample of raw EMG illustrates that when the added mass was placed mid-trunk the EMG activity is apparently more robust than when the mass is divided and carried over the two girdles (Fig. 8). Statistical analysis bears this out (Table 1, Fig. 9). In one of the four dogs, loading of the girdles actually resulted in lower muscle activity than the unloaded condition. In all four dogs, the activity of the longissimus dorsi muscle was greater when the added mass was carried mid-trunk than when the dogs ran either without added mass or with the added mass carried over the girdles (Fig. 9, Table 1). The average value of muscle activity when the added mass was carried over the girdles was 92 % of the unloaded values, while the average value of muscle activity when the added mass was carried mid-trunk was 133 % of the unloaded value.
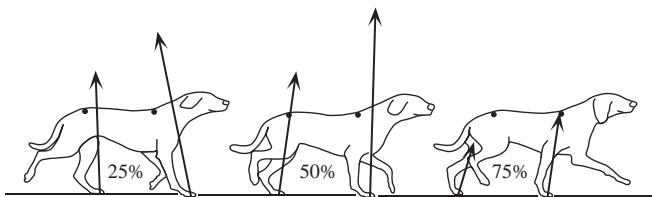
To assess whether or not the location of the added mass influenced the nature of the locomotor cycle we analyzed the effect on stride period, comparing the trials in which the dogs carried the load mid-trunk or over the girdles (control trials). For the four dogs, the average stride period of the mid-trunk trials was 0.414±0.32 s, whereas the period of the control trials was 0.418±0.30 s (P=0.71, paired t-test). This result suggests
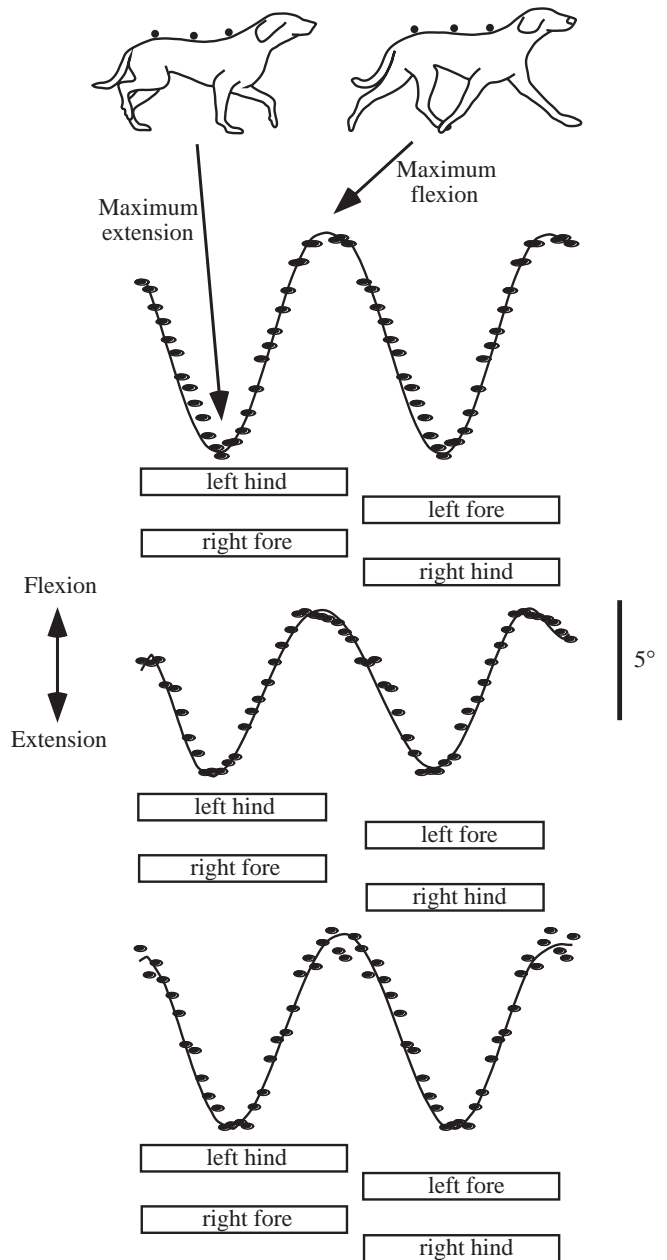

Fig. 7. The timing of dorso–ventral back kinematics relative to footfalls for three dogs trotting at their self-selected speed. Each trace follows oscillations in an angle with end-points over each girdle, with a point mid-way between the girdles as the vertex. Each trace is an average of five locomotor cycles. The time course of dorso–ventral kinematics is expressed relative to one locomotor cycle. Arrows highlight maximum extension and flexion, and are keyed to the outlines of a trotting dog taken from a video recording.

Fig. 6. Ground reaction force vectors calculated from a dog trotting over a force plate at 2.0 m s⁻¹. The lengths of the arrows indicate the magnitude of the force vectors. Filled circles indicate the approximate positions of the pectoral girdle and the iliosacral joint. Numbers indicate the percentage of the step cycle (one-half of one locomotor cycle) at which the illustrated force vectors were calculated.

Table 1. *Results of unpaired* t-*tests comparing mean rectified integrated area of the activity of the longissimus dorsi muscle in four dogs*

	Condition					
	Unloaded *versus* girdles		Unloaded *versus* mid-trunk		Girdles *versus* mid-trunk	
Animal	*t*	*P*	*t*	*P*	*t*	*P*
1	0.965	0.341	−9.742	<0.0001	−11.56	<0.0001
2	−0.27	0.788	−13.85	<0.0001	−8.23	<0.0001
3	8.92	<0.0001	−4.96	<0.0001	−11.39	<0.0001
4	−1.95	0.059	−9.48	<0.0001	−7.09	<0.0001

Unpaired *t*-tests were used to compare the unloaded condition to the girdles-loaded condition, the unloaded condition to the center-loaded condition, and the girdles-loaded condition to the center-loaded condition.

t, *t*-statistic; *P*, probability (*N*=4).

that the mechanics and kinematics of the stride were not different between the experiment and control trials.

Discussion

### *Function of the epaxial muscles in trotting dogs*

Consideration of the possible function(s) of the epaxial muscles requires an understanding of the anatomy of the axial musculoskeletal system, the activity pattern of the epaxial muscles, the time course of the major components of the ground force and how these forces may load the trunk, and how the trunk actually moves during locomotion. The gross anatomy of the epaxial muscles suggests they are involved in either extension and/or lateral flexion of the trunk. The epaxial muscles of dogs, and indeed of all vertebrates, are the only muscles dorsal to the vertebral column and ribs, and therefore are the only muscles with the anatomical configuration necessary for extension of the back.

Do the epaxial muscles extend the back during trotting? Extension occurs during approximately the first half of the support phase of a given pair of limbs (Fig. 7). Conversely, epaxial EMG occurs during approximately the second half of the support phase of a given pair of limbs (Fig. 2, Fig. 3). Therefore, the epaxial muscles are active throughout flexion of the back. Because the muscles are active during a movement they cannot produce, we conclude that the epaxial muscles are not actively producing sagittal movement of the trunk.

In addition to producing movement (performing work) during locomotion, a muscle may also oppose a movement (provide postural support). For example, the left iliocostalis muscle could be activated and shorten to produce lateral

Fig. 8. Sample raw EMG traces from a 21.6 kg dog trotting at 2.4 m s^{-1} while carrying 3.2 kg (15 % of body mass) in saddle bags on its back. Both traces are from the same electrode, implanted in the left longissimus dorsi muscle at the lumbar site. The accelerometer recordings are from an accelerometer positioned to record vertical accelerations at mid-trunk. (A) Data from a trial in which half the added mass was carried over the pectoral girdle and the other half was carried over the pelvic girdle. (B) Data from a trial in which all of the added mass was carried mid-trunk.
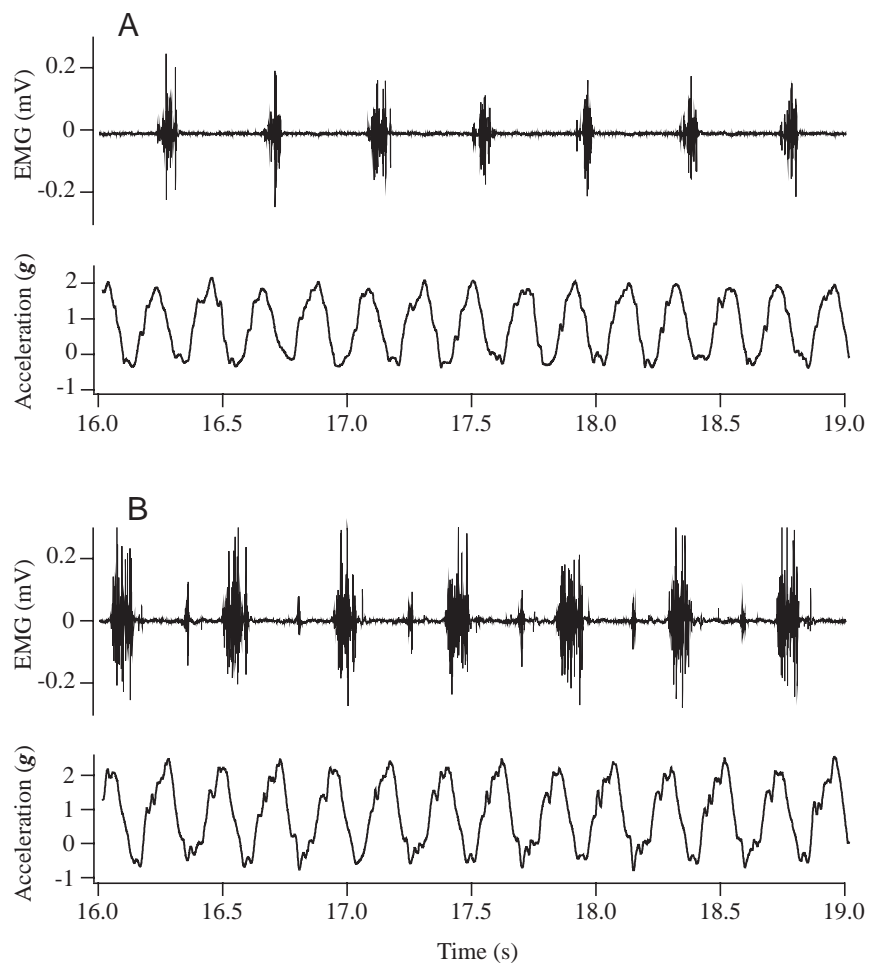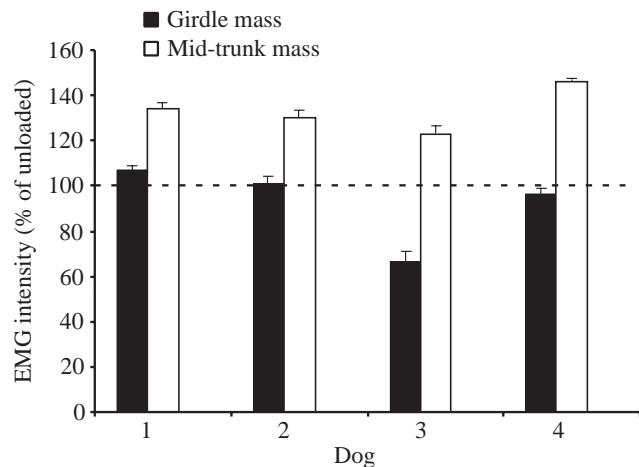
Fig. 9. Mean rectified integrated area of the of activity of the longissimus dorsi muscle in the two loaded conditions plotted as a percentage of the mean value in the unloaded condition (= 100 % EMG intensity). In three of the dogs the mean EMG activity from the girdles-loaded condition was not significantly different from the unloaded condition. In one of the dogs the mean EMG energy from the girdles-loaded condition was significantly lower than the mean EMG energy from the loaded condition. In all four dogs the mean EMG activity from the mid-trunk loading condition was significantly greater than both the unloaded condition and the girdles-loaded condition.

flexion such that the left side of the trunk becomes concave. Alternatively, the left iliocostalis muscle might be activated in order to resist forces that would cause the left side of the trunk to become convex. In fact, the usual function ascribed to the epaxial muscles of mammals, at least during walking and trotting, is that of stabilization of the trunk, and stabilization implies resistance of movement, as opposed to production of movement. We may look to the ground reaction forces and their likely effects to evaluate the possibility that the epaxial muscles function to directly counteract some component of the ground reaction forces.

The ground reaction forces that dogs produced while trotting can be divided into three components, based on their orientation to the dog. Lateral forces are those that act perpendicular to the direction the animal is moving in. The magnitude of these forces in dogs is very small (Fig. 4), and we do not consider them in this study.

Fore–aft forces act in the same direction that the animal is moving. Fore–aft force production during the support phase can be divided into deceleratory and acceleratory phases, with deceleration occurring during the first half of support and acceleration occurring during the second half (Fig. 4). What is the likely effect of these forces? Consider an animal supported by the right fore and left hind foot. During deceleration there is a rearward-directed force acting on the right side of the pectoral girdle and the left side of the pelvic girdle. These forces would tend to produce a lateral bending moment such that the left side of the trunk would become convex. In order to counteract this lateral bending moment the epaxial muscles ipsilateral to the rear foot would need to be active during the early part of

support. Muscle activity does occur ipsilateral to hindlimb support, but the activity does not begin until mid-support (Fig. 5), too late to effectively counter lateral bending of the trunk induced by deceleration. During the second half of the support phase the fore–aft force produces forward acceleration, resulting in a forward-directed force at each limb girdle. The net effect of the acceleratory forces would be a lateral bending moment such that the right side of the trunk would end up convex. In order to counteract this bending moment the epaxial muscles would need to be active contralateral to hindlimb support. While there is some activity contralateral to hindlimb support, the primary burst of activity is ipsilateral, and the timing of onset and peak of EMG is somewhat later than might be expected for counteracting lateral bending induced by forward acceleration (Fig. 5). Therefore the epaxial muscles do not appear to be counteracting lateral bending movments induced by the fore–aft component of the ground forces.

The third component of the ground reaction force is the vertical force, the force that counteracts gravity. The net effect of the vertical force on the trunk will depend on the orientation of the ground reaction force vector relative to the limb girdles. Vectors oriented between the two girdles (caudal to the pectoral and cranial to the pelvic girdles) will tend to cause both flexor and extensor moments at the intervertebral joints. Conversely, vectors oriented cranial to the pectoral girdle and caudal to the pelvic girdle would produce bending moments that would tend to cause extension of the trunk. If the vectors pass through or close to the girdles the vertical force would also tend to cause extension of the back, though to a lesser degree than if the vectors passed cranial to the pectoral and caudal to the pelvic girdles. This last possibility, the force vectors passing close to the limb girdles, is what we see in the dogs (Fig. 6). Therefore the vertical force should tend to cause extension of the back. Because the epaxial muscles are dorsal to the vertebral column, they cannot resist this tendency for back extension. Furthermore, the magnitude of the vertical force peaks at approximately mid-support, at which time the epaxial muscles have just become active (Fig. 5). Maximum activity of the epaxial muscles occurs well after peak vertical force, as the magnitude of the vertical force is decreasing. Therefore the epaxial muscles do not appear to be involved in directly resisting the action of the vertical component of the ground forces.

Given that the epaxial muscles do not appear to directly stabilize the trunk against any component of the ground forces, nor to actively produce extension of the back, what is the function of these muscles? The timing of sagittal movements of the trunk suggests they are not initiated by axial muscles, but are incidentally produced by the ground reaction forces. During the first half of diagonal limb support in the trot, the mid portion of the trunk sags ventrally due to the force of gravity (i.e. the moments resulting from the vertical component of the ground force described above, Fig. 7). In effect, dogs become slightly swaybacked during the first half of support. Then as the dog accelerates forwards and upwards during the second half of support, the back rebounds from the swayback

position and undergoes sagittal flexion. As mentioned above, the epaxial muscles are anatomically positioned to produce extension or to resist sagittal flexion of the back, and it turns out that the epaxial muscles first become active at the time that the back begins to flex out of the swaybacked (extended) position. The muscles are active throughout back flexion, and slightly after the time of maximum flexion the epaxial muscles cease activity. Thus, the epaxial muscles, whose anatomy indicates they are likely to be extenders of the trunk, are active throughout flexion of the trunk.

These data led us to the hypothesis that the epaxial muscles function to counter sagittal rebound (flexion) of the trunk during the latter half of each trotting step. We refer to the cycle of sagittal extension and flexion during each step as sagittal bounce. During the first half of limb support, the vertical force causes the trunk to sag (extend) between the girdles. During the second half, the trunk rebounds vertically (flexes). We suspect this rebound is due to the recoil of elastic elements in the ventral body wall and the vertebral column, that are stretched during the first half of support by the vertical component of the ground forces. The epaxial muscles are active during the rebound phase, suggesting they reduce flexion of the trunk.

We tested this hypothesis with the loading experiments. We reasoned that the added mass, positioned mid-trunk, would increase the loading of the elastic elements, resulting in greater sagittal bouncing of the trunk as a dog trotted. Therefore, we expected greater activity of the axial muscles that are associated with resisting sagittal rebound. We expected that the same mass carried over the girdles would not alter the sagittal bounce of the trunk and would, therefore, serve as a control for the added mass. The results of the loading experiments support our hypothesis (Table 1, Fig. 9). Adding mass over the girdles resulted in either no increase in the activity or a decrease in activity of the longissimus dorsi muscle. In all four dogs, however, placing the added mass mid-trunk caused a significant increase in muscle activity.

Evolution of epaxial muscle function in terrestrial vertebrates

The data reported here provide information relevant to the evolution of epaxial muscle function in terrestrial vertebrates. First, our data reinforce a basic dichotomy between epaxial muscle activity patterns in mammals *versus* ectothermic tetrapods (salamanders and lizards, specifically). While mammals typically exhibit biphasic activity patterns (Waters and Morris, 1972; Tokuriki, 1973a; Tokuriki, 1973b; Carlson et al., 1979; English, 1980; Thorstensson et al., 1982; Shapiro and Jungers, 1988; Shapiro and Jungers, 1994), salamanders and lizards show uniphasic patterns (Frolich and Biewener, 1992; Ritter, 1995; Ritter, 1996). Our data also reinforce a basic difference observed between anamniote and amniote tetrapods. Activity in the dorsalis trunci of the tiger salamander (*Ambystoma tigrinum*) occurs contralateral to hindlimb support (Frolich and Biewener, 1992). Conversely, activity in the epaxial muscles of lizards is ipsilateral to hindlimb support (Ritter, 1995; Ritter, 1996), as is the primary burst of activity reported here for dogs. Consequently, these data provide

evidence for a scenario of the evolution of epaxial muscle activity patterns that starts with uniphasic activity contralateral to hindlimb support (salamanders), with a major change in amniotes to activity ipsilateral to hindlimb support (lizards). This gross change in the activity of the epaxial muscles, coincident with the anatomical diversification of the epaxial muscles, appears to be associated with a change in the locomotor function of the epaxial muscles from lateral bending of the trunk in salamanders to stabilization of the trunk in lizards (Ritter, 1995; Ritter, 1996). Another major change from the ancestral pattern which appears to distinguish mammals is the addition of a second burst of activity during contralateral hindlimb support. This gross change in axial muscle activity pattern is associated with significant anatomical changes such as a more parasagittal limb posture and increased dorso-ventral flexibility of the body axis. Additional data addressing the diversity of axial muscle activity patterns in a wider range of cursorial species, as well as in species representing a more basal configuration, will be required to better understand the links between the anatomical, physiological and functional components of this locomotor complex.

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