

FUNCTION OF THE OBLIQUE HYPAXIAL MUSCLES IN TROTTING DOGS

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Summary

In trotting dogs, the pattern of activity of the obliquely oriented hypaxial muscles is consistent with the possible functions of (i) stabilization against vertical accelerations that cause the trunk to sag in the sagittal plane and (ii) stabilization against forces that tend to shear the trunk in the sagittal plane. To test these hypotheses, we compared the amount of activity of the intercostal and abdominal oblique muscles (i) when dogs carried additional mass (8–15% of body mass) supported over the limb girdles *versus* supported mid-trunk (test of sagittal bounce), and (ii) when dogs trotted up *versus* down a 10° slope (test of sagittal shear). In response to the loading manipulations, only the internal oblique muscle responded in a manner that was consistent with stabilization of the trunk against forces that cause the trunk to sag sagittally. In contrast, when the fore–aft forces were manipulated by running up and downhill, all four of the monitored muscles changed their activity in a manner consistent with stabilization of the trunk against sagittal shearing. Specifically, muscles with a craniodorsal orientation (external oblique and

external intercostal muscles) showed an increase in activity when the dogs ran downhill and a decrease when they ran uphill. Muscles with a cranioventral orientation (internal oblique and internal intercostal muscles) exhibited the opposite pattern: increased activity when the dogs ran uphill and decreased activity when they ran downhill. Changes in activity of two extrinsic appendicular muscles, the serratus ventralis and deep pectoralis, during uphill and downhill running were also consistent with the sagittal shearing hypothesis. In contrast, changes in the level of recruitment of the oblique hypaxial muscles were not consistent with stabilization of the trunk against torques that induce yaw at the girdles. Hence, we suggest that the oblique hypaxial muscles of trotting dogs act to stabilize the trunk against sagittal shearing torques induced by limb retraction (fore–aft acceleration) and protraction (fore–aft deceleration).

Key words: axial muscle, motor control, running, locomotion, electromyography, dog.

Introduction

The lateral body wall of vertebrates is composed of a variable number of parallel-fibered muscles that have oblique orientations relative to the body axis. Although this hypaxial organization is one of the defining characters of the vertebrate body (Maurer, 1896; Maurer, 1913), the functions of these muscles are poorly understood. In tetrapods, considerable attention has been given to the role these muscles play in lung ventilation (Fedde, 1976; De Troyer and Loring, 1986; Carrier, 1989; Gesell, 1936; Kadono et al., 1963; Loring and Woodbridge, 1991; Taylor, 1960; Gans and Clark, 1976; Brainerd, 1999; Simons et al., 2000). Nonetheless, because the fish ancestors of tetrapods are known to have used a buccal pump to fill their lungs (Liem, 1985; Brainerd et al., 1993), we can be confident that the basal organization of the hypaxial muscles was associated with locomotor function rather than with lung ventilation. Furthermore, in lizards, birds and mammals, locomotor recruitment of these muscles is largely dominant over recruitment for ventilation (Carrier, 1987a; Carrier, 1989; Carrier, 1990; Carrier, 1991; Carrier, 1996; Nassar, 1994; Wang et al., 1997; Owerkowicz et al., 1999; but

see Boggs et al., 1999). The absence of a ventilatory function in fishes and the predominance of the locomotor function in running tetrapods indicates that the basic architecture of the hypaxial muscles is likely to be related to locomotion rather than to breathing.

In fishes, the locomotor functions of the muscles of the back and tail have been studied relatively extensively (Bone et al., 1978; Johnsrude and Webb, 1985; Jayne and Lauder, 1994; Rome et al., 1993; Shadwick et al., 1998). To date, however, the locomotor functions of the muscles of the lateral body wall of fishes have not been addressed. In salamanders and lizards, the oblique hypaxial muscles have been associated with the production of lateral bending of the trunk (Ritter, 1996; O'Reilly et al., 2000) and with long-axis stabilization of the trunk against torsional loads (Carrier, 1990; Carrier, 1993; Bennett et al., 2001). Obviously, trotting mammals do not use their lateral hypaxial muscles to produce pronounced lateral bending, and the pattern of recruitment in trotting dogs (Carrier, 1996) suggests that torsional stabilization is not the primary locomotor function of these muscles in mammals.

These limited observations led us to suspect that the locomotor function of the oblique hypaxial muscles of mammals is different from that in ectothermic tetrapods.

This study tests two hypotheses of the function of the oblique hypaxial muscles in trotting dogs: (i) postural stabilization against vertical accelerations that cause the mid-trunk to sag and rebound in the vertical direction (sagittal bounce); and (ii) postural stabilization against fore–aft accelerations that might cause the trunk to shear in the sagittal plane (sagittal shear). Consider first the inertial forces that cause the trunk to bounce vertically during each step cycle (Ritter et al., 2001). During the first half of diagonal limb support, the inertia of the mid-trunk causes it to sag ventrally as the body decelerates in the vertical direction. 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 a small sagittal flexion. The oblique hypaxial muscles are positioned and oriented such that they could function to stabilize the trunk against the inertial forces that cause it to sag during the first half of limb support.

The forces that are expected to induce shearing of the trunk in the sagittal plane are more difficult to envisage. Extrinsic limb muscles attach the limb to the trunk and comprise most of the muscle mass of the pelvic and pectoral girdles. For the limbs to apply fore–aft forces to the ground, the extrinsic limb muscles must exert torques on the limbs. When these muscles exert torques on the limbs, they must exert equal and opposite torques on the trunk (Gray, 1968). Fore–aft ground reaction forces will induce moments on the trunk about transverse axes through the limb girdles (Fig. 1). Specifically, to accelerate in the direction of travel, legged animals must apply a posteriorly directed force to the substratum. This force is produced by extrinsic limb muscles that apply a retracting torque to the limb. The musculoskeletal anatomy of mammals suggests that limb retraction exerts torques on the trunk, as illustrated by the curved arrows in Fig. 1A. Similarly, limb-protracting torques during deceleration would exert torques on the trunk as shown in Fig. 1B. Hence, when the limbs are forcefully retracted or protracted, torques exerted by extrinsic limb muscles are expected to produce shearing forces on the trunk in the sagittal plane. These torques could be resisted by tensile elements (e.g. muscles) that have oblique orientations (Fig. 1).

To test the hypothesis that the oblique hypaxial muscles stabilize the trunk against its tendency to sag between fore- and hindlimb support, we manipulated the vertical forces imposed on the trunk of dogs during trotting. We compared the level of activity of the oblique hypaxial muscles when the dogs trotted with additional mass carried over their girdles with the level of activity from the same muscles when they carried the additional mass centered over their mid-trunk. To test the hypothesis that the oblique hypaxial muscles stabilize the trunk against forces that tend to shear it in the sagittal plane, we manipulated the fore–aft forces imposed on the trunk by having dogs trot uphill and downhill. Running uphill requires greater limb retraction forces, whereas running downhill requires

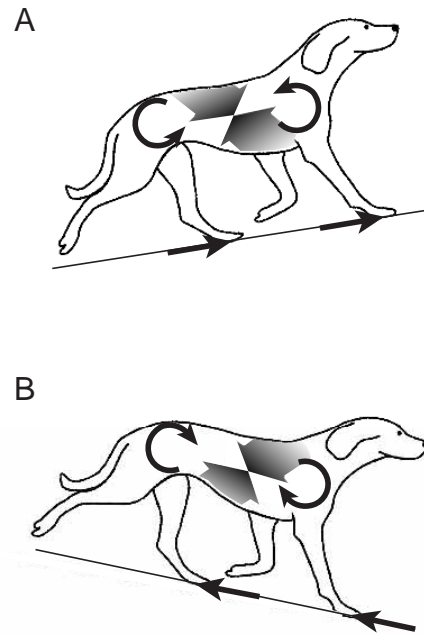


Fig. 1. Illustration of hypothesized torques exerted on the trunk (circular arrows) and requisite activity from the oblique hypaxial muscles (large gray arrows) to stabilize the trunk during running uphill (A) and downhill (B). The arrows on the substratum represent the fore–aft component of the ground reaction force. To run on hills, the extrinsic limb muscles must exert retracting or protracting torques on the limbs that results in rearward-directed forces on the ground when running uphill and forward-directed forces when running downhill. Consequently, equal and opposite torques are expected on the trunk (circular arrows). These torques tend to shear the trunk in the sagittal plane and could be resisted by contraction of the internal oblique and intercostal muscles when running uphill (A) and by the external oblique and intercostal muscles when running downhill (B).

greater limb protraction forces. Hence, we compared the level of activity of the oblique hypaxial muscles when the dogs trotted uphill *versus* downhill.

Materials and methods

Subjects

Electrical activity in the intercostal and abdominal oblique muscles was monitored in four dogs of mixed breed as they ran on a motorized treadmill. The activity of two extrinsic appendicular muscles, the serratus ventralis of the fourth rib and the deep pectoralis, were also monitored in three of the dogs. The mean body mass of the four dogs was 25.7 ± 5.7 kg (mean \pm S.D., Table 1). Dogs were obtained from local animal shelters. Each dog underwent surgical implantation of electromyographic (EMG) electrodes in the external and internal intercostal muscles of the fourth and fifth intercostal segment and in the external and internal oblique muscles in the abdominal region. Recording of muscle activity began on the second day after surgery and continued for 5–6 days. The electrodes were removed 7–8 days after implantation. After a

Table 1. *Body mass, added mass and running speeds of the four dogs*

Dog	Mass (kg)	Weight experiment, added mass		Weight experiment, running speed (m s ⁻¹)	Hill experiment, running speed (m s ⁻¹)
		(kg)	(% body mass)		
A	24.5	2.0	8.2	2.2	2.2
B	21.6	3.2	14.8	2.4	2.4
C	34.1	4.5	13.2	2.0	2.0
D	22.7	2.0	8.8	2.5	2.5

period of recovery, each dog was adopted as a pet. All procedures conformed to the guidelines of the University of Utah Institutional Animal Care and Use Committee.

Instrumentation

For surgery, subjects were initially anesthetized with an intravenous injection of Pentethal to effect. They were then intubated with an endotracheal tube and maintained on a ventilator with oxygen saturation above 90% and end tidal CO₂ below 30 mmHg and 1.0–2.0% Isoflurane for the duration of the surgery. Incisions were made through the skin above the site of electrode placement, and patch (intercostal muscles) or sew-through (oblique and appendicular muscles) 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 from 2000 or 5000 times with Grass P511 a.c. amplifiers. These signals were sampled at 4000 Hz and stored in digital form on a Macintosh computer.

Two sites in the intercostal musculature, the fourth and fifth intercostal spaces, were monitored. Two sites were implanted to provide redundancy in case of electrode failure. Patch electrodes were placed between the external and internal intercostal muscles segments (Loeb and Gans, 1986; Carrier, 1996). Electrodes were placed between the osseous portion of the ribs at the level of the insertion of the serratus ventralis muscle. Two sew-through electrodes (Basmajian and Stecko, 1962) were placed in both the external and internal oblique muscles and in two appendicular muscles: the slip of the serratus ventralis muscle inserting on the fourth rib and the deep pectoralis muscle. Electrodes in the external and internal oblique muscles were positioned in the central abdominal region at a mid-lateral location. The electrodes were constructed from 0.3 mm, multistranded, Teflon-insulated, stainless-steel wire (Cooner Wire Inc.). Patch electrodes were constructed by sewing the wire through 1 cm×3 cm rectangles of 0.8 mm Silastic sheeting (Dow Corning).

Locomotor events were recorded on video at 120 Hz with a high-speed camera (Peak Performance Technologies, Inc.). An analog signal of the locomotor cycle was obtained by monitoring the vertical acceleration of the trunk with an accelerometer (Microtron, 7290A-10) mounted on the back in the lumbar region. The video recordings were synchronized with the EMG and accelerometer recordings using a

synchronization circuit (Peak Performance Technologies, Inc.).

Force manipulations

For the purposes of experimentation, it is convenient to consider the locomotor forces against which the trunk must be stabilized as acting in three planes: vertical, fore–aft and lateral. These components of the locomotor force arise from different aspects of the locomotor cycle, and they have different phase relationships with the step cycle. Consequently, the three components of force can be manipulated independently to test hypotheses about muscle function. Among cursorial mammals, the lateral component is relatively insignificant and was not addressed in this investigation. The vertical component is by far the largest (four- to sevenfold greater than the fore–aft force) and results from accelerations associated with the rise and fall of the body during each step. During constant-speed running, the fore–aft forces result from small fore–aft accelerations that occur during each step.

To test the hypothesis that the oblique hypaxial muscles help stabilize the trunk against vertical accelerations that cause it to sag in the middle and rebound during limb support, we conducted experiments in which the trunk of the dog was loaded with 8–15% of body mass (Table 1). The dogs carried the added mass in saddlebags on their backs in two different configurations. In one case, half the added mass was carried over the pectoral girdle and the other half was carried over the pelvic girdle. In the other configuration, all the added mass was carried mid-trunk at the level of the eleventh thoracic vertebra. The activity of the intercostal and oblique muscles was recorded as the dogs ran at intermediate trotting speeds (Table 1) without the added mass, with the added mass positioned over the girdles and with the added mass positioned mid-trunk. We reasoned that the added mass, positioned mid-trunk, would produce greater sagittal bouncing of the trunk during each step and, therefore, greater activity would be required from any muscle involved in stabilizing the trunk against sagittal bouncing. We expected that trials in which the added mass was carried over the girdles would not alter the sagittal bounce of the trunk and would, therefore, serve as a control for the mass added to the mid-trunk.

In a second experiment, we recorded the electrical activity of the intercostal and oblique muscles as the dogs ran at intermediate trotting speeds (Table 1) on the level and on uphill and downhill slopes of 10°. Running up- and downhill changes the orientation of the ground force relative to the body

axis such that greater acceleration in the fore-aft direction occurs when running uphill and greater deceleration in the fore-aft direction occurs when running downhill. Consequently, this manipulation allows us to examine the effects on the oblique hypaxial muscles of changing the amplitude of the fore-aft forces.

Analysis

Timing of activity of the muscles was correlated with the period of limb support for each dog. We used the signal from the accelerometer mounted on the dog's back to divide the EMG trace into segments of one locomotor cycle duration. The EMG cycles were sampled by cutting the recording at peak vertical acceleration during left forelimb and right hindlimb support. An average signal was determined from the 15 cycles and this was plotted relative to an average cycle of limb support for each dog. Note that, because the dogs ran at a constant speed, stride duration was very uniform. Hence, an average EMG was easily calculated by adding the 15 values recorded at each sampling interval from the beginning to the end of the stride and then dividing by the sample size of 15. The average limb support cycle was determined by counting the number of video frames associated with each phase of limb support in five locomotor cycles for each dog. Synchronization of the video and EMG recordings was accomplished using a synchronization circuit (Peak Performance Technologies, Inc.) that provided an analog signal associated with every other video image.

The EMG recordings from the added-mass and hill trials were analyzed by rectifying the signal and calculating the area (V s) under the trace for individual locomotor cycles from each muscle. The signal from the accelerometer mounted on the back of the dogs was used to determine the beginning and ending of locomotor cycles. The average muscle activity (V s) was determined for each dog from 20 cycles. The average value from each dog was then used to calculate mean and standard errors from the four dogs ($N=4$). Differences among means were tested using paired *t*-tests.

Results

Oblique hypaxial muscle activity during trotting

The pattern of activity of the abdominal external oblique muscle during trotting was uniform among the four dogs (Fig. 2). The muscle exhibited one burst of activity during the first quarter of ipsilateral hindlimb support. In two of the dogs (Fig. 2A,B), activity in the muscle ended approximately halfway through ipsilateral hindlimb support. In the other two dogs, the main pulse of activity also occurred during the first half of ipsilateral hindlimb support, but the muscle remained active at a lower level for the duration of ipsilateral hindlimb support.

Three of the four dogs exhibited a very consistent pattern of activity during trotting in the abdominal internal oblique muscle. In these three dogs (Fig. 3A,C,D), there were two distinct bursts of activity. The primary burst was associated with the start and first half of ipsilateral hindlimb support, and the secondary burst occurred during the first half of

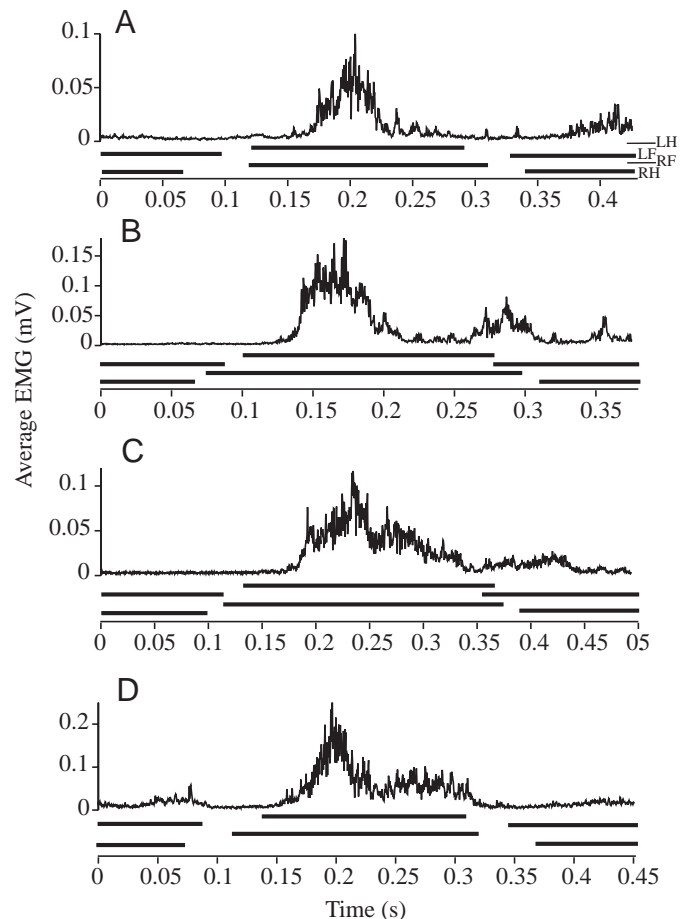


Fig. 2. Average electromyographic (EMG) activity in the left abdominal external oblique muscle from four dogs trotting at intermediate speeds. Each trace represents the average rectified signal from 15 strides. The EMG signals are plotted relative to an average limb support cycle ($N=5$) for each dog. The phases of limb support are labeled in A: LH, left hind, top trace; LF, left fore, second trace; RF, right fore, third trace; RH, right hind, bottom trace. (A) 24.5 kg dog trotting at 2.2 m s^{-1} . (B) 21.6 kg dog trotting at 2.4 m s^{-1} . (C) 34.1 kg dog trotting at 2.0 m s^{-1} . (D) 22.7 kg dog trotting at 2.5 m s^{-1} .

contralateral hindlimb support. The abdominal internal oblique muscle of the fourth dog (Fig. 3B) exhibited a single burst of activity that began during the last quarter of contralateral hindlimb support and continued through the first half of ipsilateral hindlimb support.

The fourth external intercostal muscle displayed somewhat different patterns among the four dogs during trotting (Fig. 4). Dog A exhibited two bursts of activity (Fig. 4A); one associated with the middle of ipsilateral hindlimb support, the second, and higher-amplitude, pulse associated with the first half of contralateral hindlimb support. Dog B (Fig. 4B) showed a very low amplitude pulse during the middle portion of ipsilateral hindlimb support and a much higher amplitude and longer duration pulse during the first half of contralateral hindlimb support. The external intercostal muscle of dog C (Fig. 4C) was active during the second half of ipsilateral hindlimb support and

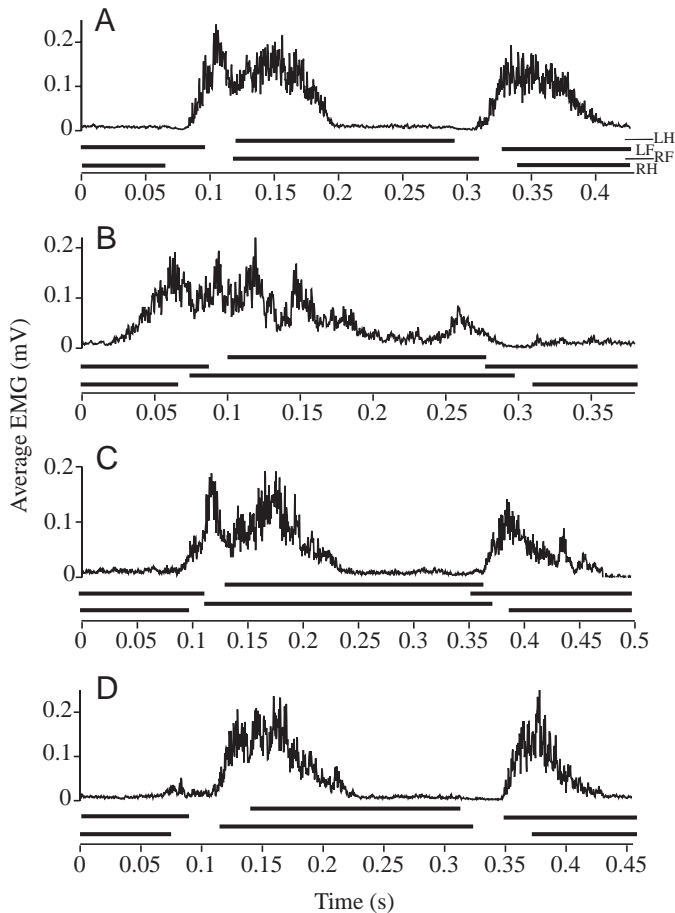


Fig. 3. Average electromyographic (EMG) activity in the left abdominal internal oblique muscle from four dogs trotting at intermediate speeds. Each trace represents the average rectified signal from 15 strides. The EMG signals are plotted relative to an average limb support cycle ($N=5$) for each dog. The phases of limb support, dog masses and running speeds are as described in Fig. 2. LH, left hind, top trace; LF, left fore, second trace; RF, right fore, third trace; RH, right hind, bottom trace.

exhibited low-level activity during the middle of contralateral hindlimb support. Dog D (Fig. 4D) displayed activity associated with the middle of ipsilateral hindlimb support.

The fourth internal intercostal muscle showed the greatest variation in activity of the four muscles that we monitored (Fig. 5). In all four dogs, there was significant activity during the last portion of contralateral hindlimb support and the beginning of ipsilateral hindlimb support. Dog B, however, differed from the other three in that the primary pulse began earlier, during the middle of contralateral hindlimb support (Fig. 5B). Dog D differed from the other three in having a large burst of activity associated with the beginning of contralateral hindlimb support (Fig. 5D).

Muscle activity during trotting with mass added to the trunk

If a muscle were to assist in stabilizing against the tendency of the trunk to bounce sagittally during each step, we would expect that muscle to exhibit greater activity when mass was

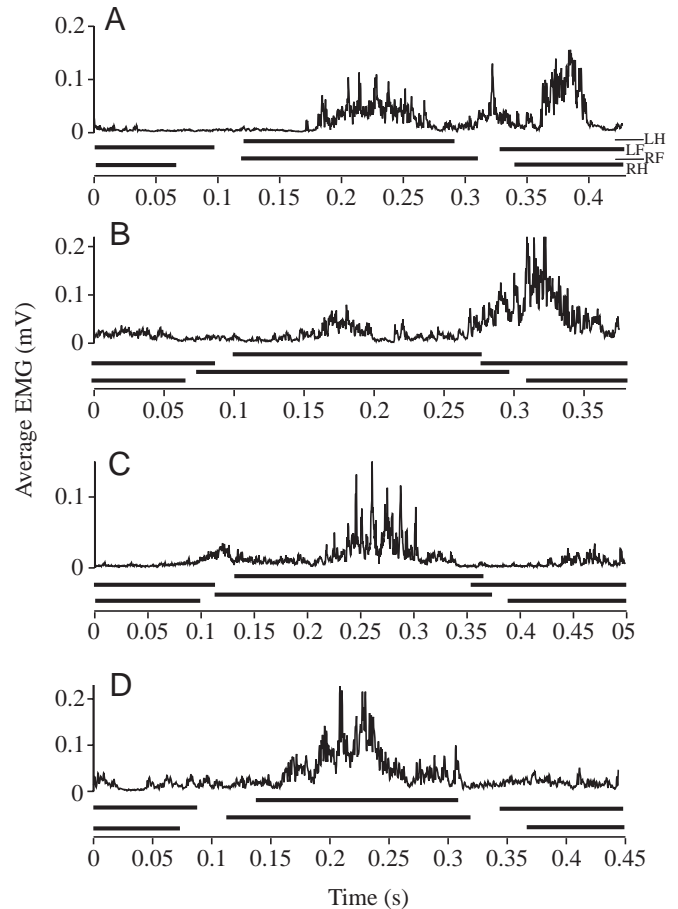


Fig. 4. Average electromyographic (EMG) activity in the left fourth external intercostal muscle from four dogs trotting at intermediate speeds. Each trace represents the average rectified signal from 15 strides. The EMG signals are plotted relative to an average limb support cycle ($N=5$) for each dog. The phases of limb support, dog masses and running speeds are as described in Fig. 2. LH, left hind, top trace; LF, left fore, second trace; RF, right fore, third trace; RH, right hind, bottom trace.

added to the middle of the trunk than when it was added to the girdles. Two of the oblique muscles we monitored did show a trend in this direction (Fig. 6). The internal oblique muscle displayed greater activity when the added mass was carried mid-trunk than over the girdles ($P=0.041$). The external oblique muscle also appeared to display greater activity when the added mass was carried mid-trunk than over the girdles, but this result was not significant ($P=0.135$). In contrast, activity in the external intercostal and internal intercostal muscles increased above that of the unloaded trials to roughly the same extent regardless of whether the mass was positioned mid-trunk or carried over the girdles ($P=0.420$ and $P=0.326$ respectively).

The two appendicular muscles responded to the added mass manipulation in much the same manner (Fig. 7A). In the three dogs in which we monitored activity of the serratus ventralis and deep pectoralis muscles, activity of both muscles increased to approximately the same extent ($P>0.2$) when the

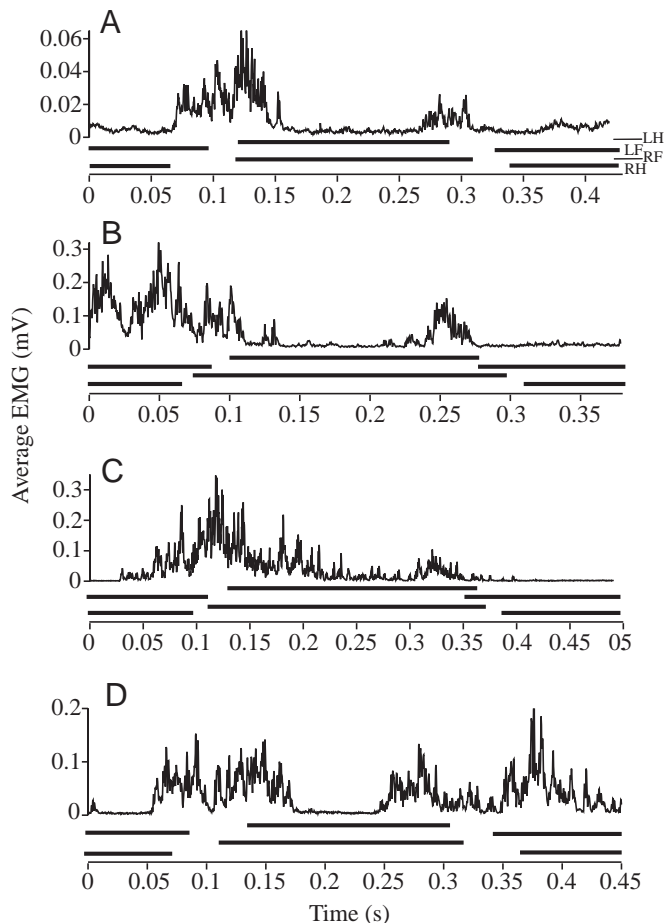


Fig. 5. Average electromyographic (EMG) activity in the left fourth internal intercostal muscle from four dogs trotting at intermediate speeds. Each trace represents the average rectified signal from 15 strides. The EMG signals are plotted relative to an average limb support cycle ($N=5$) for each dog. The phases of limb support, dog masses and running speeds are as described in Fig. 2. LH, left hind, top trace; LF, left fore, second trace; RF, right fore, third trace; RH, right hind, bottom trace.

added mass was carried mid-trunk as when it was carried over the girdles.

Muscle activity during trotting uphill and downhill

Muscles with fibers that run from caudoventral towards craniodorsal, hereafter called 'craniodorsal orientation' (i.e. external oblique and external intercostal muscles), showed an increase in activity when the dogs ran downhill and a decrease when they ran uphill (Fig. 8). Muscles with fibers that run caudodorsal towards cranioventral, hereafter called 'cranioventral orientation' (i.e. internal oblique and internal intercostal muscles), exhibited the opposite pattern: increased activity when the dogs ran uphill and decreased activity when they ran downhill. Specifically, compared with running on the level, running uphill was associated with a decrease in activity in the external oblique ($P=0.050$), but no change in the amount of activity in the external intercostal muscles ($P=0.269$)

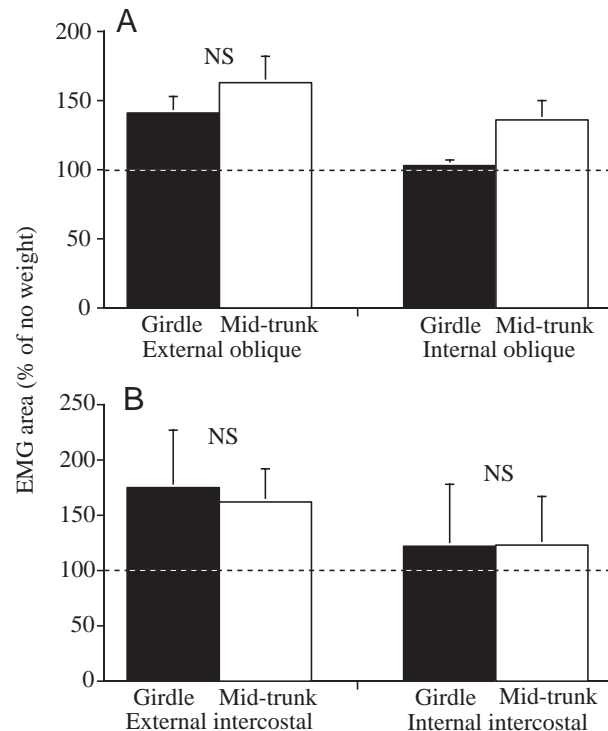


Fig. 6. Bar charts of the average activity of the oblique (A) and intercostal (B) muscles from four dogs during trotting while carrying additional mass distributed over the pectoral and pelvic girdles (filled columns) and centered over the middle of the trunk (open columns). Values are means + S.E.M. The rectified and integrated area of 20 stride cycles was averaged for each dog, and an average value was then calculated from the mean values of the four dogs ($N=4$). Results are presented as a percentage of values obtained when the dogs trotted without additional mass. Paired t -tests were used to evaluate whether there was a significant difference between the girdle and mid-trunk trials. Muscles with P -values of greater than 0.05 were taken to be not significantly different and are marked NS.

(Fig. 9). Running downhill resulted in a marked increase in activity over running on the level in both the external oblique ($P=0.043$) and external intercostal ($P=0.041$) muscles. In contrast, running uphill was associated with an increase in activity in the internal oblique ($P=0.002$) and internal intercostal ($P=0.018$) muscles. Running downhill produced a decrease in activity compared with running on the level in the internal oblique ($P=0.013$) and internal intercostal ($P=0.069$) muscles (Fig. 9).

The two extrinsic appendicular muscles also exhibited a dramatic response to trotting uphill and downhill in the three dogs that were monitored (Fig. 7B). Relative to trotting on the level, the serratus ventralis muscle displayed a trend of decreased activity when trotting uphill ($P=0.088$) and a trend of increased activity when trotting downhill ($P=0.112$). The deep pectoralis muscle exhibited the opposite pattern; an increase in activity when trotting uphill ($P=0.028$) and a trend towards a decrease when trotting downhill ($P=0.063$).

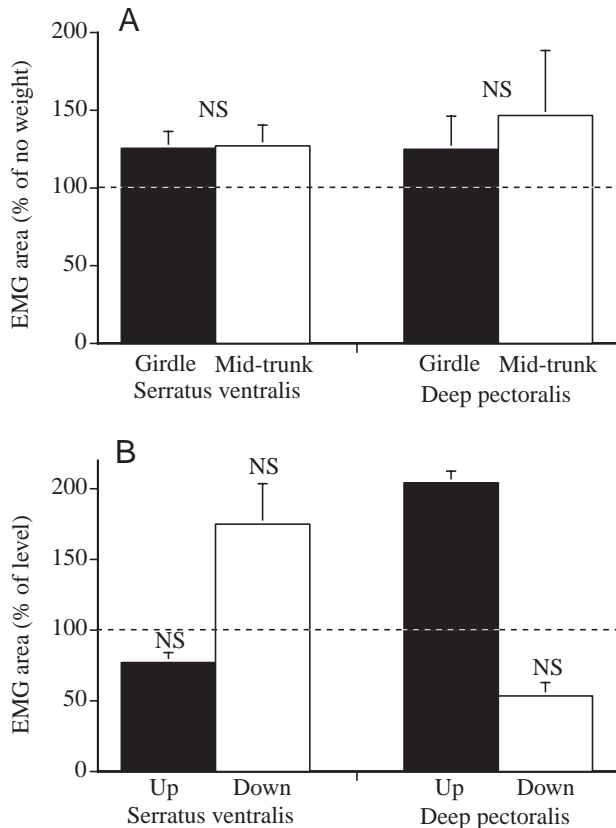


Fig. 7. Bar charts of the average activity of the serratus ventralis and deep pectoralis muscles from three dogs during trotting while (A) carrying additional mass divided between the girdles or over the mid-trunk and (B) while running uphill and downhill. Values are means + S.E.M. The rectified and integrated area of 20 stride cycles was averaged for each dog, and an average value was then calculated from the mean values of the three dogs ($N=3$). Results are presented as a percentage of values obtained when the dogs trotted without additional mass (A) or trotted on the level (B). Paired t -tests were used to evaluate whether there was a significant difference between the girdle and mid-trunk trials (A) and between the slope and level trials (B). Muscles with P -values of greater than 0.05 were taken to be not significantly different and are marked NS.

Discussion

The hypaxial muscles of the lateral body wall of fishes and many ectothermic tetrapods appear to help produce lateral bending of the trunk and may, therefore, contribute to the production of locomotor work. In contrast, the trunk of trotting mammals is held relatively rigid (Pridmore, 1992) and does not produce work. In trotting mammals, activity in the oblique hypaxial muscles must, therefore, be related to postural support.

Postural stabilization against long-axis torsion of the trunk

During trotting, the vertical component of the ground force could influence trunk posture in two ways. First, because the trunk of trotting tetrapods is supported by diagonal limbs (right fore- and left hindlimb, or left fore- and right hindlimb), the vertical component could induce long-axis torsion in the trunk

(Carrier, 1990). If muscles stabilized the trunk against torsion, they would have to have oblique orientations, and the oblique hypaxial muscles could, in theory, accomplish this postural support. If this were true, the internal oblique and internal intercostal muscles ipsilateral to hindlimb support would have to generate force simultaneously with the external oblique and external intercostal muscles contralateral to hindlimb support. The oblique hypaxial muscles of walking lizards (Carrier, 1990) and salamanders (Carrier, 1993; Bennett et al., 2001) show a pattern of activity that is consistent with this type of force generation and have been suggested to function to provide postural support against long-axis torsion.

The oblique hypaxial muscles of trotting dogs, however, exhibit a pattern of activity that appears inconsistent with postural support against forces that would induce torsion in the trunk. In only one of the four dogs tested (dog A) were the external intercostal and internal oblique muscles active simultaneously in the correct phase relationship with limb support to stabilize the trunk against torsion. Given that the expected pattern for torsional stabilization (i) was observed in only one of the four dogs, (ii) was observed in only two of the four muscles monitored in this dog, and (iii) accounted for only part of the activity displayed by these two muscles, we suspect that stabilization of the trunk against torsion is not the primary function of the oblique hypaxial muscles in trotting dogs. Nevertheless, the possibility that the oblique hypaxial muscles of mammals provide torsional stabilization during trotting warrants further attention.

Postural stabilization against sagittal bouncing of the trunk

The second way in which the oblique hypaxial muscles could help to stabilize the trunk against perturbations induced by the vertical component of the locomotor force is by resisting the tendency of the trunk to bounce vertically in the sagittal plane. During the beginning of a trotting step, the vertical force causes the trunk to sag between forelimb and hindlimb support. Then, during the second half of the step, the trunk tends to rebound vertically. It has been suggested that the epaxial muscles stabilize the trunk against the sagittal rebound in trotting dogs (Ritter et al., 2001). It is possible that the oblique hypaxial muscles could provide postural support against the initial sag of the trunk at the beginning of the step. The external and internal oblique and internal intercostal muscles all exhibited activity at the beginning of limb support that might act to resist the tendency of the trunk to sag between fore- and hindlimb support.

To test the possibility that the oblique hypaxial muscles function to stabilize the trunk against sagittal sagging, we loaded the trunk of trotting dogs with additional mass and monitored the activity of the oblique muscles. If a hypaxial muscle were to assist in stabilizing against the tendency of the trunk to sag during the beginning of a trotting step, we would expect that muscle to show greater activity when the added mass was carried mid-trunk than when the added mass was carried over the girdles. Only the external and internal oblique muscles exhibited this pattern when mass was added mid-

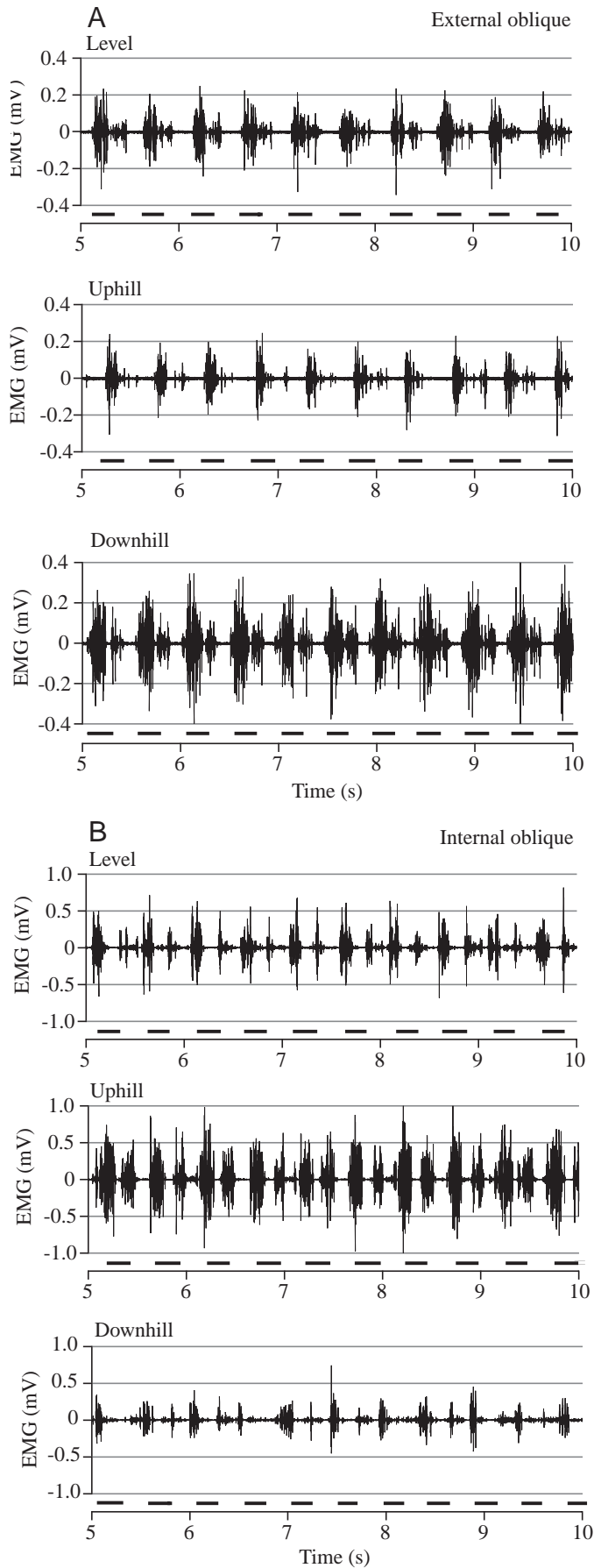


Fig. 8. Sample electromyographic signals of the external (A) and internal (B) oblique muscles recorded during running on the level, uphill and downhill. These recordings are from a 34 kg dog running at 2 ms^{-1} . They illustrate the different patterns displayed by the external *versus* the internal hypaxial muscles. In each graph, the horizontal bars represent the period of support of the left hindlimb. Compared with running on the level, activity in the external oblique muscles decreased when the dogs ran uphill and increased when the dogs ran downhill. In contrast, the internal oblique muscles displayed the opposite pattern.

trunk; the result for the external oblique muscle, however, was not statistically significant. The intercostal muscles displayed equivalent increases in activity in response to both mid-trunk and girdle weights.

The architecture of the internal oblique muscle is more appropriate for stabilization against sagittal sag than that of the other oblique muscles. It originates mainly from the tuber coxae of the iliac spine and its fibers run cranioventrally to insert on the linea alba. Hence, its activity at the beginning of limb support could help resist the tendency of the trunk to sag. The architecture of the internal oblique muscle, its pattern of activity early in support, and the increased activity when the added mass was carried mid-trunk suggest that the internal oblique muscle helps to stabilize the trunk against vertical accelerations that cause sagging in the sagittal plane.

Postural stabilization against lateral bending and sagittal shearing

Extrinsic limb muscles attach the limb to the trunk and comprise most of the muscle mass of the pelvic and pectoral girdles. For the limbs to apply fore–aft forces to the ground, the extrinsic limb muscles must exert torques on the limbs. When these muscles exert torques on the limbs, they must exert equal and opposite torques on the trunk (Gray, 1968). If the trunk is to be kept more-or-less rigid during trotting, it must be stabilized against forces and torques that tend to deform it. We explored two postural stability problems that may be related to the fore–aft ground reaction force during trotting.

Fore–aft ground reaction forces could induce moments about a vertical axis through the girdle (i.e. yaw) and, hence, cause the trunk to bend laterally (Carrier, 1990). Stabilization of the trunk against yawing moments would require force generation by lateral hypaxial muscles ipsilateral to hindlimb support early in the step, followed by force generation from the lateral hypaxial muscles contralateral to hindlimb support during the middle and second half of a step. In trotting dogs, the internal oblique and internal intercostal muscles are active early in ipsilateral hindlimb support. Hence, the timing of activity of these two muscles appears to be appropriate to stabilize the trunk against yawing moments on the trunk.

Fore–aft ground reaction forces will also induce moments on the trunk about transverse axes through the limb girdles. When the limbs are forcefully retracted or protracted, torques exerted by extrinsic limb muscles are expected to produce sagittal shearing forces on the trunk (Fig. 1). To accelerate in

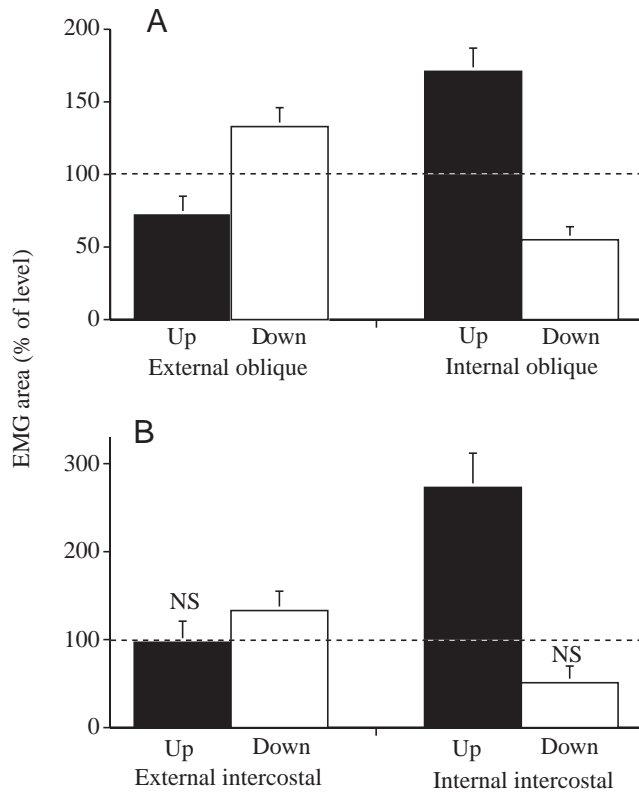


Fig. 9. Bar charts of the average activity of the oblique (A) and intercostal (B) muscles from four dogs during running uphill (filled columns) and downhill (open columns). Values are means + S.E.M. The rectified and integrated area of 20 stride cycles was averaged for each dog, and an average value was then calculated from the mean value of the four dogs ($N=4$). Results are presented as a percentage of values obtained during running on the level. Paired t -tests were used to evaluate whether there was a significant difference between the slope and level trials. Muscles with P -values of greater than 0.05 were taken to be not significantly different and are marked NS.

the direction of travel (as in uphill running), legged animals must apply a posteriorly directed force to the substratum. In mammals, this force is produced by extrinsic limb muscles that apply a retracting torque to the limb. The manner in which the extrinsic limb muscles load the trunk of running lizards and mammals has been studied in a few species (Jenkins and Weijs, 1979; Goslow et al., 1981; Jenkins and Goslow, 1983). These studies and the musculo-skeletal anatomy suggest that limb retraction exerts torques on the trunk as illustrated by the curved arrows in Fig. 1A. Similarly, limb-protracting torques during deceleration are expected to exert torques on the trunk as shown in Fig. 1B. These torques would tend to induce sagittal shearing of the trunk that could be resisted by tensile elements (e.g. muscles) that have oblique orientations.

To determine whether the oblique hypaxial muscles provide postural support against moments that cause yawing and/or sagittal shearing of the trunk, we manipulated the fore-aft forces by having the dogs trot uphill and downhill. When running on level surfaces, animals exert no net fore-aft force to maintain a steady speed. In contrast, running on an incline

requires a net fore-aft force to overcome some component of the force of gravity. Because the fore-aft forces are greater when animals run on an incline, recruitment of muscles associated with fore-aft postural control can be expected to increase. This manipulation should also allow us to distinguish between the two hypotheses presented above because stabilization of the trunk against yawing moments is expected to require different patterns of muscle recruitment from those required for stabilization against sagittal shearing. If the oblique hypaxial muscles were used to stabilize the trunk against yawing moments at the girdles, we would expect a simultaneous increase in activity in both the external and internal hypaxial muscles; first ipsilateral, and then contralateral, to hindlimb support. However, if the hypaxial muscles provided stability against torques that caused fore-aft shearing of the trunk, we would expect opposite patterns from the external and internal hypaxials. Specifically, we would expect the external hypaxial muscles (i.e. those with a craniodorsal orientation) to exhibit greater activity when the dogs trotted downhill (Fig. 1B) and the internal hypaxial muscles (those with a cranioventral orientation) to exhibit greater activity when the dogs trotted uphill (Fig. 1A).

In response to this manipulation, the oblique hypaxial muscles of the four dogs displayed a recruitment pattern that was not consistent with the hypothesis of stabilization against yawing moments at the girdles, but was consistent with the hypothesis of stabilization against sagittal shearing. When the dogs ran uphill, the external oblique and external intercostal muscles exhibited reduced activity or no change in activity compared with running on the level, and the internal oblique and internal intercostal muscles exhibited increased activity. When the dogs ran downhill, the pattern was reversed. The external oblique and external intercostal muscles showed elevated activity compared with level running and the internal oblique and internal intercostal muscles displayed reduced activity.

Changes in the pattern of activity of the two extrinsic appendicular muscles were also consistent with the hypothesis that hypaxial muscles resist sagittal shearing due to protracting and retracting torques exerted on the limbs. The serratus ventralis and deep pectoralis muscles exhibited opposite responses to uphill and downhill trotting. Relative to level running, the serratus ventralis muscle showed decreased activity when the dogs ran uphill and increased activity when the dogs ran downhill (although neither change was significant). The deep pectoralis exhibited the opposite pattern: increased activity during uphill trotting and decreased activity during downhill trotting. Provided that the axis of rotation of the forelimb is somewhere between the insertion sites in the serratus ventralis and deep pectoralis muscles, the increased activity in the serratus ventralis during downhill running is probably associated with the production of greater limb protraction torques. Similarly, the increase in activity in the deep pectoralis muscle during uphill running is almost certainly associated with the production of greater limb retraction torques. Hence, the changes in activity in these two muscles appear to be consistent with the generation of the hypothesized

torques exerted on the trunk during uphill and downhill running (circular arrows in Fig. 1).

Concluding remarks

Manipulation of the vertical forces applied to the trunk of trotting dogs indicates that the internal oblique muscles, and possibly the external oblique muscles, are involved in stabilization against vertical accelerations that cause the mid-trunk to sag between the limb girdles early in each trotting step. Manipulation of the fore–aft ground forces in trotting dogs indicates that the oblique hypaxial muscles function as a group to stabilize the trunk against torques that tend to induce sagittal shearing of the axial musculoskeletal system. Whether or not the oblique hypaxial muscles stabilize the trunk against sagittal shearing torques in other species and in behaviors other than trotting warrants further investigation.

In spite of anatomical similarities, the locomotor activity and function of the oblique hypaxial muscles appears to be highly variable among the few tetrapod species that have been studied. In the two species of salamander that have been studied (*Dicamptodon ensatus* and *Ambystoma tigrinum*), the oblique hypaxial muscles appear to provide torsional stability and produce lateral bending of the trunk during walking (Carrier, 1993; O'Reilly et al., 2000; Bennett et al., 2001). The pattern of activity in walking iguanas (*Iguana iguana*) is also consistent with torsional stabilization (Carrier, 1990). However, at least one of the oblique hypaxial muscles, the external oblique, is clearly associated with the production of lateral bending in two lizards, *Iguana iguana* and *Varanus salvator* (Ritter, 1996). In trotting domestic dogs, the only mammal for which there are observations, the oblique hypaxials appear not to be involved in torsional stabilization or in the production of lateral bending. Instead, they appear to provide postural stabilization of the trunk against forces and torques that tend to produce sagging of the trunk between the girdles and shearing of the trunk in the sagittal plane. These differences in the function of the oblique hypaxial muscles probably reflect the extent to which the axial musculoskeletal system contributes to the production of locomotor work during trotting (Rockwell et al., 1938; Gray, 1968; Rewcastle, 1981) as well as evolutionary changes associated with the ability to run and breathe at the same time in the lineage that gave rise to mammals (Carrier, 1987b; Bramble and Jenkins, 1989).

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