Hypaxial muscle activity during running and breathing in dogs

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Summary

The axial muscles of terrestrial vertebrates serve two potentially conflicting functions, locomotion and lung ventilation. To differentiate the locomotor and ventilatory functions of the hypaxial muscles in mammals, we examined the locomotor and ventilatory activity of the trunk muscles of trotting dogs under two conditions: when the ventilatory cycle and the locomotor cycle were coupled and when they were uncoupled. Patterns of muscle-activity entrainment with locomotor and ventilatory events revealed (i) that the internal and external abdominal oblique muscles performed primarily locomotor functions during running yet their activity was entrained to expiration when the dogs were standing, (ii) that the internal and external intercostal, external oblique thoracic and transversus abdominis muscles performed both locomotor and respiratory functions simultaneously, (iii) that the parasternal internal intercostal muscle performed a primarily respiratory function (inspiration) and (iv) that the deep pectoralis and longissimus dorsi muscles performed only locomotor functions and were not active while the dogs were standing still. We conclude that the dual function of many hypaxial muscles may produce functional conflicts during running. The redundancy and complexity of the respiratory musculature as well as the particular pattern of respiratory–locomotor coupling in quadrupedal mammals may circumvent these conflicts or minimize their impact on respiration.

Key words: hypaxial muscle, ventilation, locomotion, locomotor–respiratory coupling, mammal, dog, *Canis familiaris*.

Introduction

The hypaxial muscles of terrestrial vertebrates are known to function in both lung ventilation and locomotion. A costal mechanism that employs both the intercostal and oblique hypaxial muscles, as well as the rectus abdominis and transversus abdominis muscles, is well established (De Troyer and Loring, 1986) and is thought to represent a basal ventilatory mechanism for amniotes (Liem, 1985; Carrier, 1989; Brainerd, 1999). In addition, in amphibians, which do not posses lateral ribs and inspire *via* a buccal pump, the transversus abdominis muscle has been shown to contribute to the production of expiratory airflow (Brainerd, 1998; Brainerd and Monroy, 1998; Simons et al., 2000). Some role in locomotion has been identified for the intercostal, oblique and transversus abdominis muscles in salamanders (Carrier, 1993; Bennett et al., 2001), lizards (Carrier, 1990; Ritter, 1995, 1996), domestic dogs (Carrier, 1996; Fife et al., 2001), humans (Morris et al., 1961; Zetterberg et al., 1987; McGill, 1991; Gardner-Morse and Stokes, 1998; Davis and Mirka, 2000) and birds (Nassar, 1994; Boggs, 1997; Boggs et al., 1999). In humans, the transversus abdominis and the diaphragm function in both ventilation and stabilization of the trunk during limb movements, but the abdominal oblique muscles appear to adopt solely a postural function during arm movements (Hodges et al., 1997; Hodges and Gandevia, 2000). Hence, the function of the hypaxial muscles in locomotion of tetrapods has been only partially elucidated, but appears to vary among the taxa that have been studied.

The dual role of the hypaxial muscles poses a problem for sustained locomotion because potentially conflicting demands placed on the hypaxial muscles in a running tetrapod would be expected to compromise their locomotor or ventilatory actions. Consistent with the possibility of conflicting demands is the observation that the hypaxial muscles of lizards abandon their ventilatory function during moderate-speed and rapid running (Carrier, 1989, 1990, 1991). The loss of ventilatory function by the hypaxial muscles in running lizards is associated with reduced costal ventilation (Carrier, 1987a, 1991; Wang et al., 1997; Owerkowicz et al., 1999) and has been suggested to represent an evolutionary constraint on the aerobic capacity and locomotor stamina of lizards (Carrier, 1987b, 1991). The intercostal muscles of dogs have also been shown to abandon ventilatory function when ventilatory and locomotor cycles become uncoupled during trotting (Carrier, 1996); however, costal ventilation in dogs appears to be less affected by locomotion than in lizards and is augmented by the ventilatory action of the diaphragm muscle (Ainsworth et al., 1996). In contrast to that of the interosseus intercostals, the activity of the parasternal portions of the internal intercostal muscles of dogs remains entrained to ventilation, specifically inspiration, rather than locomotion when breathing becomes uncoupled

(Carrier, 1996), and the activity of the transversus abdominis remains entrained to both expiration and stride events (Ainsworth et al., 1996). Nevertheless, the nature of the dual role of many of the hypaxial muscles and the implications for locomotor behavior and performance remain poorly understood.

The two groups of tetrapods that are capable of sustained vigorous locomotion, mammals and birds, entrain their ventilatory and locomotor cycles when they run. During running, birds and trotting mammals often couple at one breath per step (2:1) or one breath per stride (1:1) (Bramble and Carrier, 1983; Bramble and Jenkins, 1989; Nassar et al., 2001). Bounding gaits, such as galloping, are associated with 1:1 coupling, in which expiration occurs as the back flexes in the sagittal plane during forelimb support and inspiration occurs as the back extends during hindlimb support. Flying birds exhibit a wide variety of coupling patterns from one breath per locomotor cycle (1:1) to one breath per five locomotor cycles (1:5) (Berger et al., 1970; Boggs, 1997). In all cases, coupling represents strict phase locking of respiratory events to specific locomotor events. Although the physiological significance of coupling is not well understood (Lee and Banzett, 1997), the hypothesis that it bestows some selective advantage is supported by the observations that coupling appears to have evolved independently in birds and mammals and that, in both mammals and running birds, the natural frequency of the locomotor cycle and the resonant frequency of the respiratory system are tuned to the same value (Young et al., 1992; Nassar et al., 2001). One advantage of breathing in a coupled pattern is that it may minimize potential conflict between locomotor and respiratory events such that those muscles that effect both ventilation and locomotion can operate economically (Funk et al., 1997). Evaluation of the hypothesis that coupling reduces locomotor–ventilatory conflict is currently limited, in part, by our lack of understanding of the dual function of the hypaxial musculature during running and breathing.

We undertook this study to differentiate the locomotor and ventilatory functions of the hypaxial muscles in running mammals, i.e. to identify those muscles that are primarily locomotor, those that are primarily ventilatory and those with a dual function. In particular, we were interested in the functions of the external and internal oblique muscles that had not been studied in mammals other than humans. We monitored ventilation and the activity of the major hypaxial muscles in dogs trotting on a motorized treadmill. We searched for associations between the timing of the activity of individual muscles and the locomotor or ventilatory cycle by taking advantage of fact that dogs sometimes uncouple their breathing and locomotor cycles such that the phase relationship of the two cycles changes over time.

Materials and methods

Muscle activity was recorded in four mixed-breed dogs (*Canis familiaris*) while they stood and ran at moderate trotting speeds on a motorized treadmill. The mean body mass of the four dogs was 25.7 ± 5.7 kg (mean ± S.D.). Each dog was obtained from local animal shelters and trained to run on the treadmill. Electrodes were implanted surgically in eight trunk muscle and one appendicular muscle. 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 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. They were then intubated with an endotracheal tube and maintained on a ventilator with oxygen to 1.3 MAC (minimal alveolar concentration) and 1–2 % 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. Electrodes were constructed from 0.3 mm diameter, multistranded Teflon-insulated stainless-steel wire (Cooner Wire, Inc.; part AS636). Lead wires from the electrodes were passed subcutaneously to a dorsal exit point just caudal to the dorsal tips of the scapulae. Electromyographic (EMG) signals were passed through a separate shielded, lightweight cable for each electrode (Cooner Wire, Inc.; part NMUF2/30-404b SJ), filtered above 1000 Hz and below 100 Hz, and amplified approximately 2000 or 5000 times with Grass P511 AC amplifiers. These signals were sampled at 4000 Hz and stored in digital form on an Apple Macintosh computer.

Two sites in the intercostal musculature, the fourth and fifth intercostal spaces, were monitored in all 4 dogs. Two sites were implanted to provide redundancy in case of electrode failure. Patch electrodes were placed between the external and internal intercostal muscle segments (as described in Loeb and Gans, 1986; Carrier, 1996). Electrodes were placed between the osseous portion of the ribs, at the level of the insertion site of the serratus ventralis muscle. Two sew-through electrodes were placed in the thoracic and abdominal external oblique, internal oblique, transversus abdominis muscles (all 4 dogs), two in the longissimus dorsi muscles (3 dogs) and in one appendicular muscle, the deep pectoralis muscle (2 dogs). Electrodes in the external oblique thoracic muscle were placed in the slips that inserted on ribs four and five. Electrodes in the abdominal external and internal oblique and transversus abdominis muscles were positioned in the central abdominal region at a mid-lateral location. The electrodes in the longissimus dorsi muscle were placed mid-trunk at approximately the level of the eleventh thoracic vertebra. Patch electrodes were constructed by sewing the wire through 1 cm×3 cm rectangles of 0.8 mm Silastic sheeting.

Locomotor events were recorded on video with a high-speed camera (Peak Performance Technologies, Inc.) at 120 fields s^{-1}. 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.).

Ventilatory airflow was measured with a biased-flow mask pneumotachograph. To allow the dogs to breathe and pant as naturally as possible, the mask covered the entire face and was big enough to allow the mouth to open and the tongue to hang out of the mouth. The mask was held in place by a snug collar around the neck and was sealed around the head just in front of the ears with an inflatable rubber tube. The bias flow was supplied to the mask with two 1.83 m lengths of 35 mm (internal diameter) breathing tube (666120, Hans Rudolph, Inc.) glued to the top surface of the mask. The input tube from the mask was connected to a pneumotachograph (4813, Hans Rudolph, Inc.) with a linear capacity up to $800 \, l \, min^{-1}$. An additional 0.61 m length of breathing tube was connected to the upstream side of the pneumotachograph, making the total length of tubing on the upstream side of the mask 2.44 m. The output tube from the mask was connected to a constant-flow vacuum controlled by a rheostat that produced a bias flow that ranged from 2 to $41 \, s^{-1}$, depending on the dog. Pressure changes across the pneumotachograph were measured with an Omega 176 differential pressure transducer, with a range of $\pm 1.75 \, kPa$ ($\pm 17.8 \, cmH_2O$).

Analysis of electromyographic data

To examine the relationships between EMG bursting pattern and ventilation and locomotion, we generated ensemble averages (Banzett et al., 1992a,b) of periodic muscle activity for each muscle from 27–32 samples per muscle. Ensemble averages were generated from rectified EMG signals using two different types of sampling window: (i) extending from the time of peak expiratory airflow to the next peak expiratory airflow, and (ii) extending from the time of peak vertical acceleration of forelimb support contralateral to the electrodes to the next peak vertical acceleration of contralateral forelimb support (Fig. 1). Ensemble averages were generated from trials in which the phase relationship between the ventilatory and locomotor cycles drifted relative to one another (uncoupled) and from trials in which ventilation and locomotion were phase-locked to one another (coupled). Both types of sampling window were used for uncoupled trials. For coupled trials, because ventilation and locomotion were locked in phase, ensemble averages generated relative to the ventilatory cycle (type i, above) and those generated relative to the stride (type ii, above) would be identical. Therefore, we sampled only relative to stride. Three different ensemble averages were thus generated for each muscle from each dog: (i) coupled, sampled relative to stride, hereafter called the coupled average; (ii) uncoupled, sampled relative to breath, called the uncoupled breath average; and (iii) uncoupled, sampled relative to stride, called the uncoupled stride average.

The distinction between coupled and uncoupled trials was based on examination of the relative durations of the ventilatory and locomotor cycles and their relative timing. When one looks at the ventilation and acceleration traces, it is immediately obvious whether a dog's breathing is coupled or uncoupled to locomotor events. In a sample of 15 steps of coupled locomotion from one dog, for example, the timing of a ventilatory event, peak expiratory airflow, relative to a locomotor event, mid-stance of the left forelimb, showed a standard deviation of 6.7 ms. The steps had a mean duration of 240 ms. The ratio of these values reveals a 2.8 % drift in the relative timing of locomotor and ventilatory events during coupled locomotion. In contrast, during uncoupled locomotion, in which locomotor and ventilatory cycles have different periods, ventilation can drift by 100 % in as few as four steps (for examples of coupled and uncoupled trials, see Fig. 3 in Carrier, 1996). Even slight differences in ventilatory and locomotor periods resulted in an obvious shift of the two signals when examined over several strides, so periods of coupled and uncoupled breathing were easily and reliably identified.

EMG signals within a sampling window varied in duration and consequently differed in the number of recorded points. To enable averaging across multiple samples of different durations, EMG signals were re-sampled by linear interpolation using a custom-built LabVIEW program to produce signals 800 points in length regardless of the original length. Ensemble averages were generated by averaging the value for each of the 800 points across multiple (27–32) samples for a given muscle EMG. The result was a series of 800 points that represented the average activity of the muscle during the period of interest (i.e. peak expiration to peak expiration or peak vertical acceleration to peak vertical acceleration) (Fig. 1). The ensemble averages also facilitated comparison among dogs and trials.

Ensemble averages generated relative to breathing (i.e. uncoupled breath averages) allowed us to examine the relationship between muscle activity and ventilation, i.e. to determine whether EMG activity was concentrated in or absent from particular periods of the breathing cycle. If EMG activity were correlated with the breathing cycle, we would expect the ensemble average of uncoupled breaths to show areas of increased activity and areas of little or no activity. If activity were to occur independently of the breathing cycle, we would expect a flat, noisy trace with no areas of concentrated high-amplitude activity. Similarly, ensemble averages of uncoupled trials generated relative to the stride (i.e. uncoupled stride averages) should show periodic increases in activity if the muscle activity was associated with locomotion, or flat, noisy traces if there was no association.

To prevent a biased representation in our ensemble averages of activity occurring during (or absent from) different regions of our sampling window, we 'whitened' the data from uncoupled breathing trials by sampling equally from several locomotion/ventilation phase relationships for each ensemble average. Thus, all phase relationships of drifting bursts of
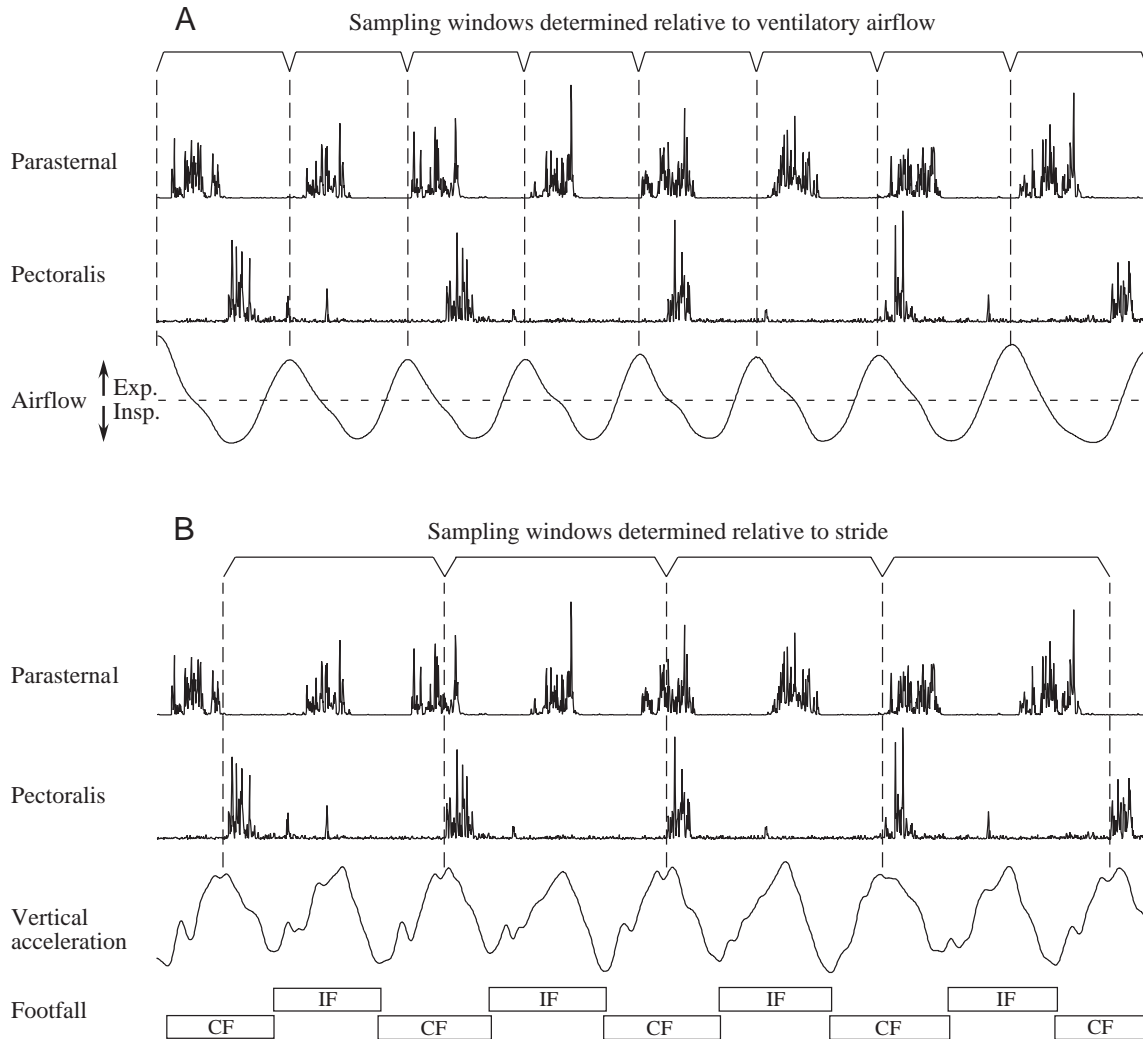
Fig. 1. Representative electromyographic (EMG) traces from two muscles with traces for ventilatory airflow and vertical acceleration of the trunk illustrating the ensemble averaging method of analysis. The rectified EMG signal is sampled relative to ventilation in windows extending between peaks of expiratory airflow (A). In this case, the parasternal is entrained to ventilation and the bursts do not shift within the sampling window, while the bursts of the pectoralis do. The same EMG signals are also sampled relative to the stride in windows extending between peaks of vertical acceleration during contralateral forelimb support (B). Here, the pectoralis remains locked to the stride and its bursts do not shift relative to the sampling windows, but the bursts of the parasternal do. Traces in A and B are aligned in time. Footfall patterns of the forelimbs are shown at the bottom, with boxes labeled IF indicating the period of ipsilateral forelimb support and boxes labeled CF indicating contralateral forelimb support. See Materials and methods for further explanation. Exp., expiration; Insp., inspiration.

activity were 'captured' with equal frequency in each part of the sampling window. 'Whitening' was not necessary for coupled breathing trials because locomotion and ventilation were locked to one another (i.e. no drifting of EMG activity occurred).

An average for each of the three different ensemble averages was generated across all dogs for each muscle to examine overall patterns. Prior to averaging across dogs, the ensemble averages for each dog were normalized to a percentage of maximum activity by dividing each value in each ensemble average by the maximum value obtained for that dog, whether that maximum be in the coupled average, uncoupled breath average or uncoupled stride average. By averaging normalized values, the pattern from one dog would not overwhelm the

pattern from another (because of differences in EMG signal strength among electrodes, for example).

Interpretation of ensemble averages

Four combinations of phasic activity in the uncoupled ensemble averages are possible: phasic activity in neither uncoupled breath average nor uncoupled stride average, activity in uncoupled breath average, activity in uncoupled stride average and activity in both uncoupled averages. In the simplest case, the first possibility, a pattern of no bursting in either the uncoupled stride average or the uncoupled breath average would indicate that the muscle functions in neither locomotion nor ventilation. The second possibility, a bursting pattern in the breath average, for example, and no bursting in
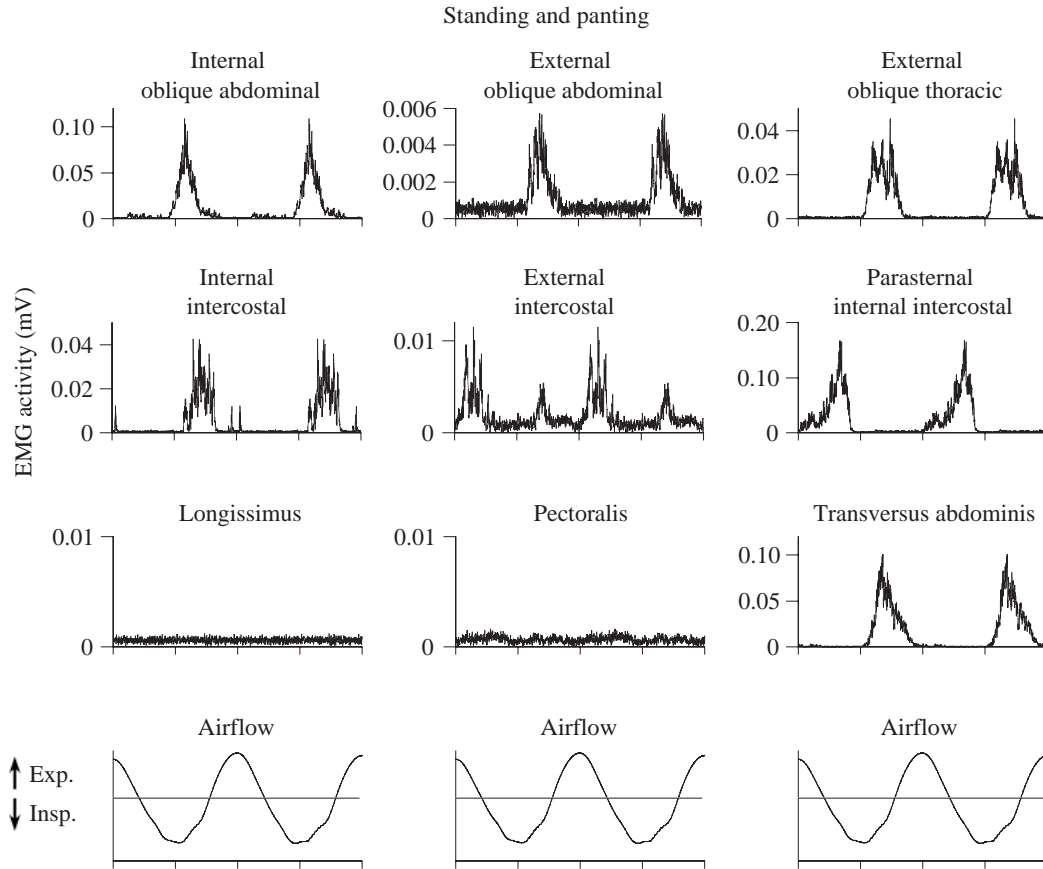
Fig. 2. Ensemble averages of electromyographic (EMG) activity of nine trunk muscles from a single dog standing and panting, revealing a ventilatory function for all muscles except the longissimus dorsi and deep pectoralis. Only the external intercostal and parasternal internal intercostal have an inspiratory function. Muscles that were active were not all active at the same time. Ventilatory airflow traces are shown below for reference. Exp., expiration; Insp., inspiration. All traces are on the same time scale. See text for discussion.

the corresponding stride average, would indicate that the muscle (i) has a ventilatory function and is active periodically to power ventilation, and (ii) has no consistent locomotor function. Alternatively, a bursting pattern in the uncoupled stride average and no bursting in the corresponding breath average would reveal that the muscle (i) has a locomotor function and is turned on to power locomotion, and (ii) has no consistent ventilatory function. The third possible pattern, bursting in both averages, would indicate that the muscle has both functions and is active to contribute to both ventilation and locomotion.

When the activities of the muscles during standing and panting (i.e. during only ventilatory function) and in coupled averages are considered together with these four patterns from running and breathing, muscles can be placed into four functional categories. (i) Pure locomotor function; no bursting during standing and panting, but bursting in the uncoupled stride average and no bursting in the uncoupled breath average. This pattern would indicate that the muscle is active at the appropriate time to perform a locomotor function and has no effect on ventilation. (ii) Primarily locomotor function; bursting during standing and panting and bursting in the uncoupled stride average and coupled average, and no bursting

Table 1. *Coefficients of determination (r^2) for the comparisons between coupled and uncoupled stride averages and between coupled and uncoupled breath averages for each muscle*

Muscle	Stride	Breath
External intercostal	0.28	0.07
Internal intercostal	0.83	0.06
Parasternal internal intercostal	0.001	0.35
External oblique thoracic	0.49	0.29
External oblique abdominal	0.88	0.14
Internal oblique abdominal	0.88	0.07
Transversus abdominis	0.83	0.79
Deep pectoralis	0.72	0.02
Longissimus dorsi	0.96	0.003

in the uncoupled breath average. This pattern would reveal that, although the muscle functions during ventilation when the dogs are not running, the muscle takes on a locomotor function and abandons its ventilatory function during trotting. (iii) Dual function; bursting during standing and panting, as well as in both uncoupled averages; this pattern would suggest that the muscle is active during trotting only when it can contribute to both ventilatory and locomotor functions. (iv) Ventilatory

function; bursting during standing and panting, and in the uncoupled breath average and coupled average, but not in the uncoupled stride average. This pattern would show that the muscle is active when it needs to contribute to ventilation, regardless of its effect on locomotion.

These four categories illustrate the different potential responses of muscles to functional conflicts. If a muscle were to have a primarily locomotor function, it would have a ventilatory function during rest, but the locomotor function would override it during running. In other words, the bursts of activity would drift relative to the breath cycle, at times assisting in ventilation and at times hindering it. Activity would be independent of ventilation, which would presumably be effected by other muscles. Another possible response to functional conflict would be to adjust the timing or duration of bursts to reduce the conflict, as might occur in muscles with a dual function. Thus, we expect that a shift in timing of bursts relative to stride or ventilation from coupled to uncoupled running would indicate a functional conflict (i.e. a burst shifts in the uncoupled breath or stride average from its position in the coupled average to avoid conflict), but not one severe enough to necessitate complete abandonment of one function as in muscles with a primarily locomotor function.

The effects of coupled *versus* uncoupled breathing on the EMG pattern of each muscle were examined quantitatively by a modification of the methods of Farley and Koshland (2000). For each muscle, Pearson correlations (r) were determined for the uncoupled stride average *versus* the coupled stride average and for the uncoupled breath average *versus* the coupled breath average (coupled breath averages were obtained by re-sampling coupled stride averages relative to breath). Each correlation coefficient was then squared to yield the coefficient of determination (r^2), which indicates the proportion of the point-to-point variation in the uncoupled ensemble average that is explained by variation in the coupled ensemble average. A high r^2 indicates that the two ensemble averages are similar and that uncoupled breathing has little effect on the pattern of muscle activity. A low r^2 indicates that the ensemble averages are different, either because the temporal pattern of bursting is effected by coupling or because the muscle shows no bursting in the uncoupled average.

Results

Dogs displayed both coupled and uncoupled breathing patterns during trotting. During uncoupled breathing, they breathed in a pattern of more than one step per breath, and breaths were not aligned with a particular phase of the locomotor cycle. Once the dogs had warmed up, they exhibited the more typical, stereotyped pattern of coupled breathing, which consisted of one breath per step. During coupled breathing, peak inspiratory airflow occurred just before or at peak vertical acceleration consistently in all dogs. In ensemble averages obtain from coupled breathing (i.e. coupled averages),
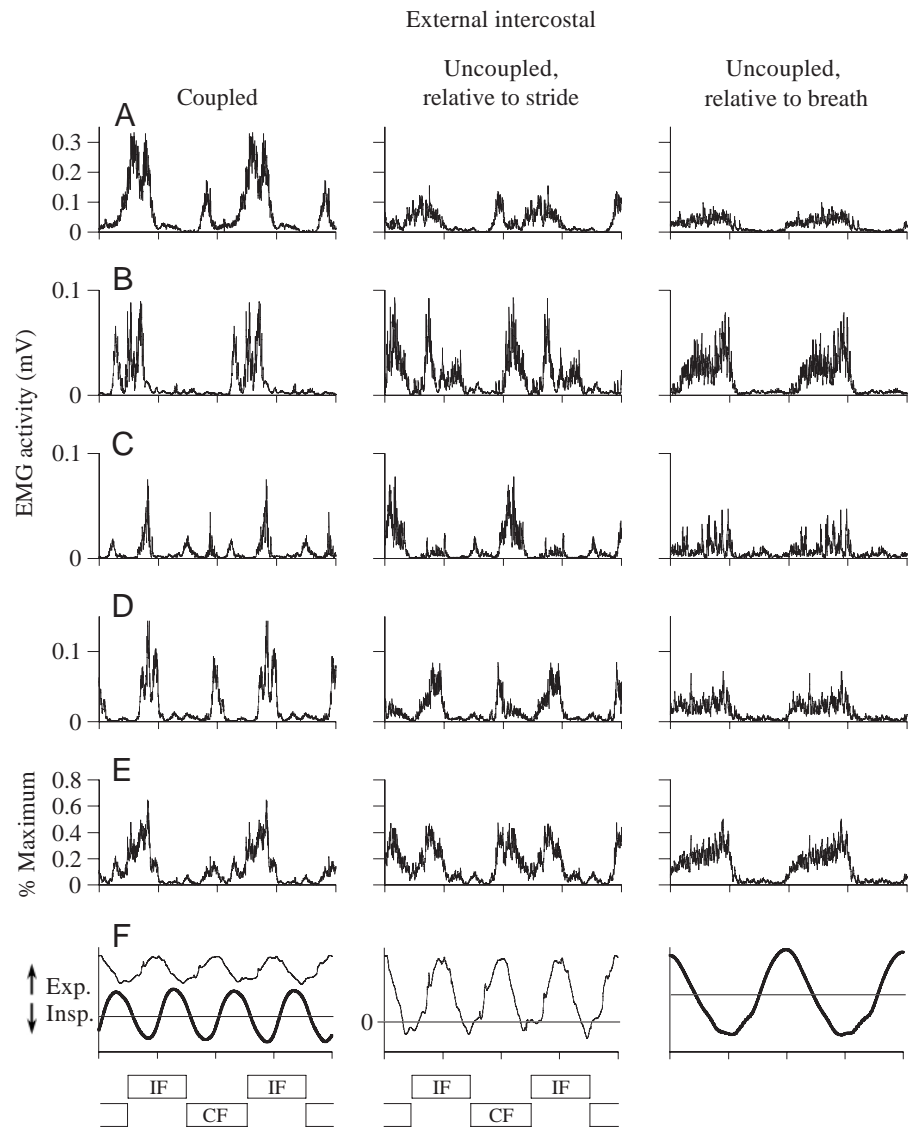

Fig. 3. Ensemble averages of electromyographic (EMG) activity of the external intercostal muscle. The pattern of bursting in uncoupled breath averages is similar in all dogs, and its relationship to ventilation reveals an inspiratory function for this muscle. The pattern of activity averaged relative to the stride is more variable, but a clear bursting pattern is present, indicating a locomotor function. Samples are from four dogs (A–D), and the average across four dogs (E), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (F). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

bursting was evident in all muscles examined, indicating a ventilatory or locomotor role, or both roles, for all muscles.

During panting while standing still, several muscles showed activity associated with ventilatory events (Fig. 2). The internal oblique abdominal, external oblique abdominal, external oblique thoracic, internal intercostal and transversus abdominis showed activity in the latter half of inspiration and the beginning of expiration; this pattern is consistent with an expiratory function for these muscles. Two muscles, the parasternal portion of the internal intercostal and the external intercostal, were active out of phase with the other muscles, showing bursts that extended from the second half of expiration to the beginning of inspiration. This pattern is appropriate for generating inspiratory airflow. These muscles were never all active simultaneously, however, and appeared to trade off from minute to minute as the dogs changed posture slightly. Fig. 2 shows the pattern of activity that each muscle showed when it was active, but this figure should not be interpreted to indicate that all the muscles shown were active at the same time. The longissimus dorsi and pectoralis showed no activity while the dogs were standing still.

During running, the transversus abdominis, external intercostal, internal intercostal, parasternal internal intercostal and external oblique thoracic muscles showed phasic activity in uncoupled ensemble averages sampled relative to both ventilation and locomotion. Only two hypaxial muscles showed phasic activity in uncoupled ensemble averages sampled only relative to locomotion during running: the internal oblique abdominal and the external oblique abdominal. The coefficients of determination (r^2) that indicate the degree to which the locomotor and ventilatory activity of each muscle is influenced by the pattern of breathing (coupled *versus* uncoupled) are listed in Table 1. The pattern of activity of each muscle during running is described below.

External intercostal

The external intercostal muscle showed phasic activity in both uncoupled breath and stride averages (Fig. 3). Among coupled averages, there was a great deal of variation from dog to dog, with 1–4 bursts of activity. The largest burst was associated with the flight phase and the first half of ipsilateral forelimb support and occurred during the second half of expiration and the first half of inspiration.

The shorter, lower-amplitude bursts were associated with mid-contralateral forelimb support and were centered on peak inspiratory airflow. The coupled average of all dogs (Fig. 3E) showed a large burst associated with the first half of ipsilateral forelimb support and a much smaller burst centered on mid-contralateral forelimb support. In uncoupled stride averages, the bursts were more variable and dispersed in time than in coupled averages. The greatest activity was generally associated with mid-contralateral forelimb support, and smaller bursts were associated with mid-ipsilateral forelimb support. The uncoupled stride average pattern from all dogs (Fig. 3E) showed two bursts per stride, the larger burst
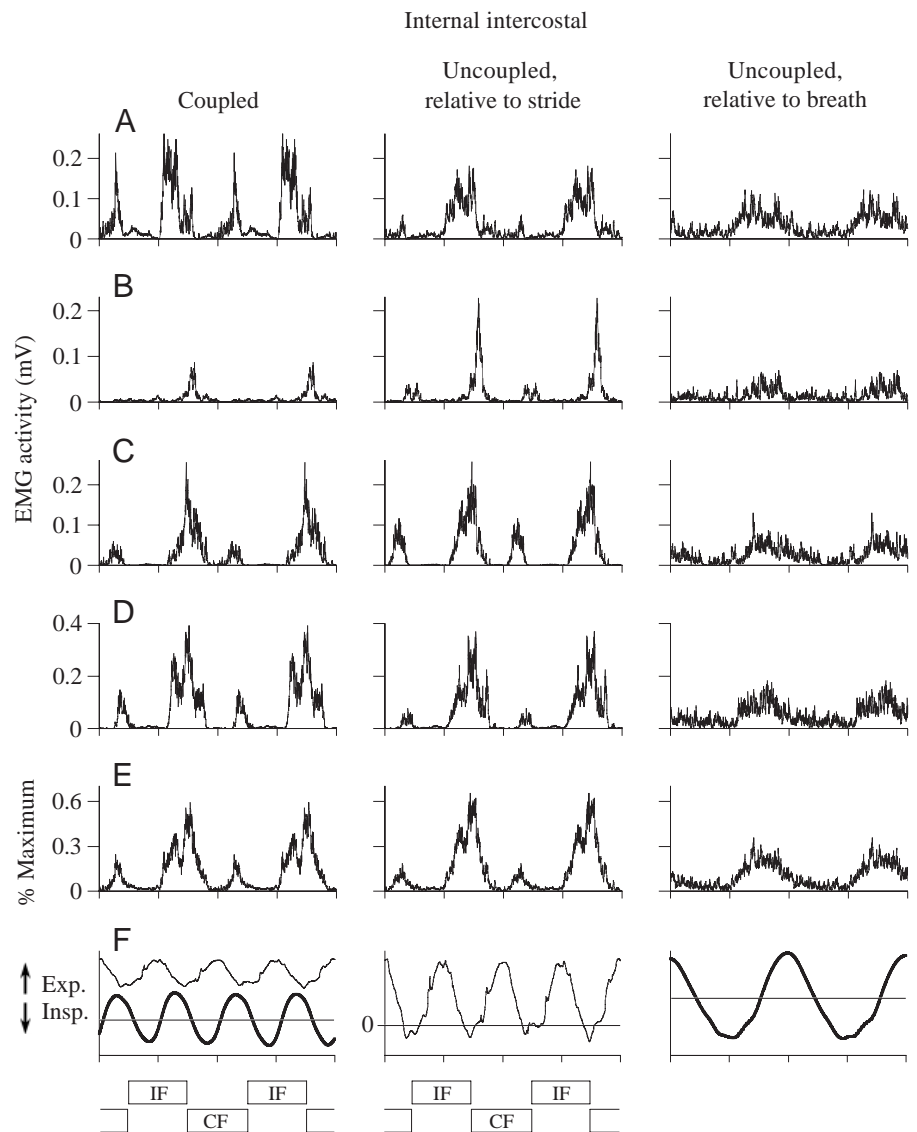

Fig. 4. Ensemble averages of electromyographic (EMG) activity of the internal intercostal muscle. The patterns are similar for all dogs, indicating an expiratory function as well as a locomotor function. Samples are from four dogs (A–D), and the average across four dogs (E), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (F). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

associated with mid-contralateral forelimb support and the slightly smaller burst associated with the first half of ipsilateral forelimb support. In uncoupled breath averages, increased activity was evident extending from peak expiratory airflow to peak inspiratory airflow in all dogs. This pattern is consistent with an inspiratory function. During standing and panting (Fig. 2), activity also occurred appropriately for inspiration.

Internal intercostal

The internal intercostal muscle showed phasic activity in both the uncoupled breath averages and the uncoupled stride averages, but the stride averages showed a much stronger pattern. The patterns of the EMGs in the uncoupled stride averages were very similar to the coupled averages (Fig. 4, first two columns). There were typically two bursts of activity, both centered on peak expiratory airflow during coupled breathing. The shorter, lower-amplitude burst occurred at the transition from contralateral to ipsilateral forelimb support. The larger burst was centered at the transition from ipsilateral to contralateral forelimb support and extended from mid-ipsilateral support to mid-contralateral support at its greatest extent. In the uncoupled breath averages (Fig. 4, third column), activity was not as concentrated into bursts as in coupled breathing, but a low-amplitude single period of increased activity was evident extending from peak inspiratory airflow to peak expiratory airflow, indicative of an expiratory function. Activity appropriate for expiration also occurred during this period when the dogs were standing (Fig. 2).

Parasternal internal intercostal

The parasternal portion of the internal intercostal muscle showed bursting in coupled averages, uncoupled breath averages and uncoupled stride averages (Fig. 5). In coupled averages, the largest burst was associated with the first half of contralateral forelimb support and the smaller bursts were associated with the beginning of ipsilateral support. In uncoupled stride averages, the bursts were not as clean or as consistent among dogs as was the case in the coupled averages. The largest burst was associated with the second half of contralateral forelimb support in one dog, the second half of ipsilateral support in

one dog and the transition from ipsi- to contralateral support in one dog, and there were no clear bursts in the fourth dog. The uncoupled stride average from all dogs (Fig. 5E) showed little bursting because of the high degree of variation among dogs. In uncoupled breath averages, bursts were similar in all dogs: bursts extended from peak expiratory airflow to peak inspiratory airflow, consistent with an inspiratory function. The dog that showed no bursting in its stride average showed the strongest, cleanest bursting in the breath average. Bursts were much clearer during coupled than during uncoupled breathing,
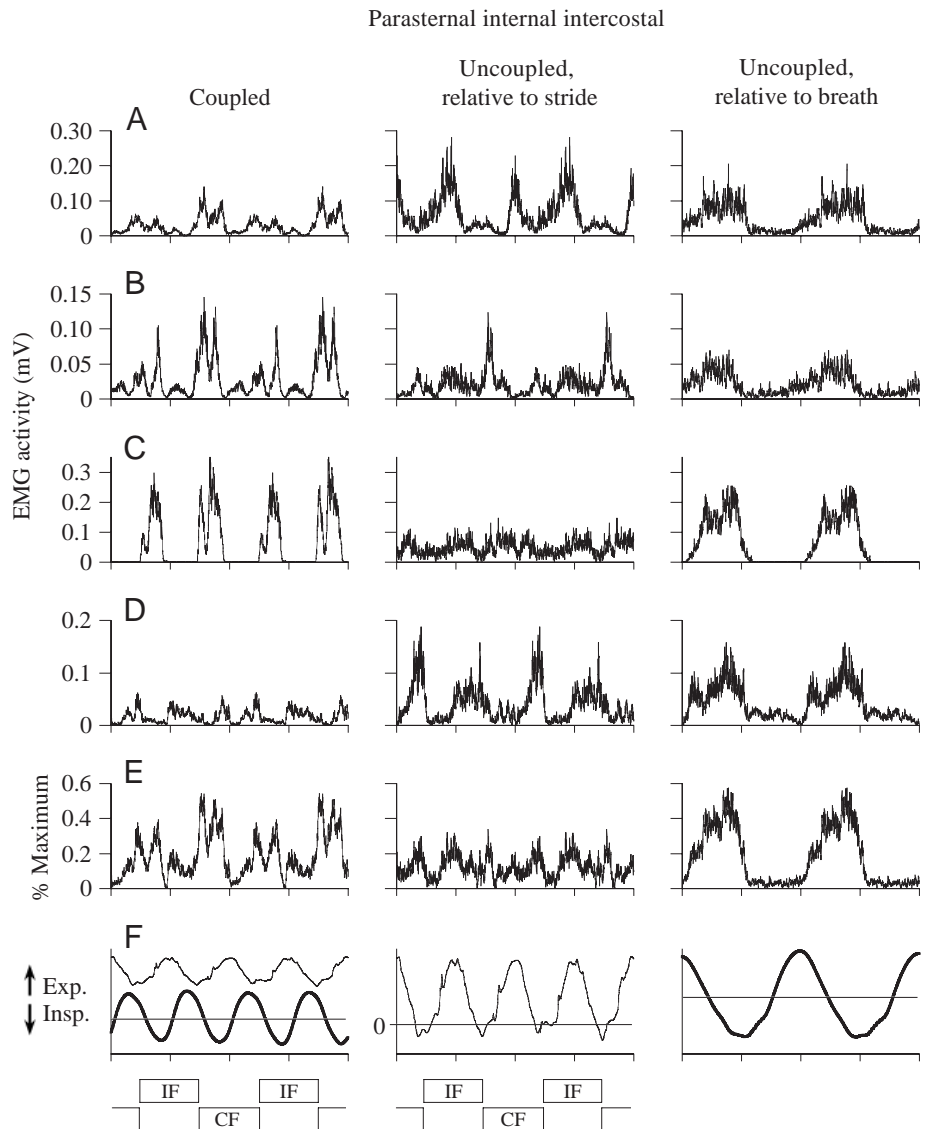

Fig. 5. Ensemble averages of electromyographic (EMG) activity of the parasternal portion of the internal intercostal muscle. The bursting pattern is consistent in uncoupled breath averages, indicating a clear inspiratory function for this muscle. The bursting is much more variable in uncoupled stride averages and almost undetectable in the average across all dogs (E), indicating a variable or sporadic locomotor function that may be different in each dog. Samples are from four dogs (A–D), and the average across four dogs (E), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (F). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

indicating that the relationship between breathing and stepping during coupled breathing was appropriate for both locomotor and ventilatory activity in this muscle, and some interference occurred during uncoupled breathing. During standing and panting (Fig. 2), activity was also appropriate for inspiration.

External oblique thoracic

The external oblique thoracic muscle showed phasic activity in both uncoupled stride averages and breath averages (Fig. 6). A burst was present centered on or near each forelimb support in coupled averages. In uncoupled stride averages, the burst associated with ipsilateral forelimb support was consistently larger. Uncoupled breath averages showed bursts extending from peak inspiratory airflow to peak expiratory airflow, consistent with an expiratory function. As in both the external oblique abdominal and internal oblique abdominal muscles, activity during rest (Fig. 2) indicates an expiratory function for the external oblique thoracic muscle.

External oblique abdominal

The external oblique abdominal muscle showed phasic activity in uncoupled stride averages and very little phasic activity in uncoupled breath averages (Fig. 7). In coupled and uncoupled stride averages, the largest spike was centered on mid-contralateral forelimb support, and a secondary burst was associated with the start of ipsilateral forelimb support. In one dog, the secondary burst was as large as the primary burst and longer in duration. Uncoupled breath averages showed no bursting and only a slight increase in activity during inspiration in one dog. These patterns reveal that the external oblique abdominal muscle is primarily a locomotor muscle and has little if any ventilatory function during running. During rest (Fig. 2), activity occurred during the latter half of inspiration, consistent with a role in expiration.

Internal oblique abdominal

The internal oblique abdominal muscle showed phasic activity in uncoupled stride averages and very little in uncoupled breath averages (Fig. 8), a pattern similar to that of the external oblique abdominal. The largest burst in the stride averages was associated with

the first half of contralateral forelimb support, and a secondary burst was sometimes present in association with the first half of ipsilateral forelimb support. This pattern was virtually identical to that in the coupled averages. Uncoupled breath averages showed no clear bursts, although a slight increase in activity was evident in one dog in association with the latter half of inspiratory airflow. The ensemble averages considered together indicate that the internal oblique abdominal muscle has primarily a locomotor role during running. During standing and panting (Fig. 2), activity
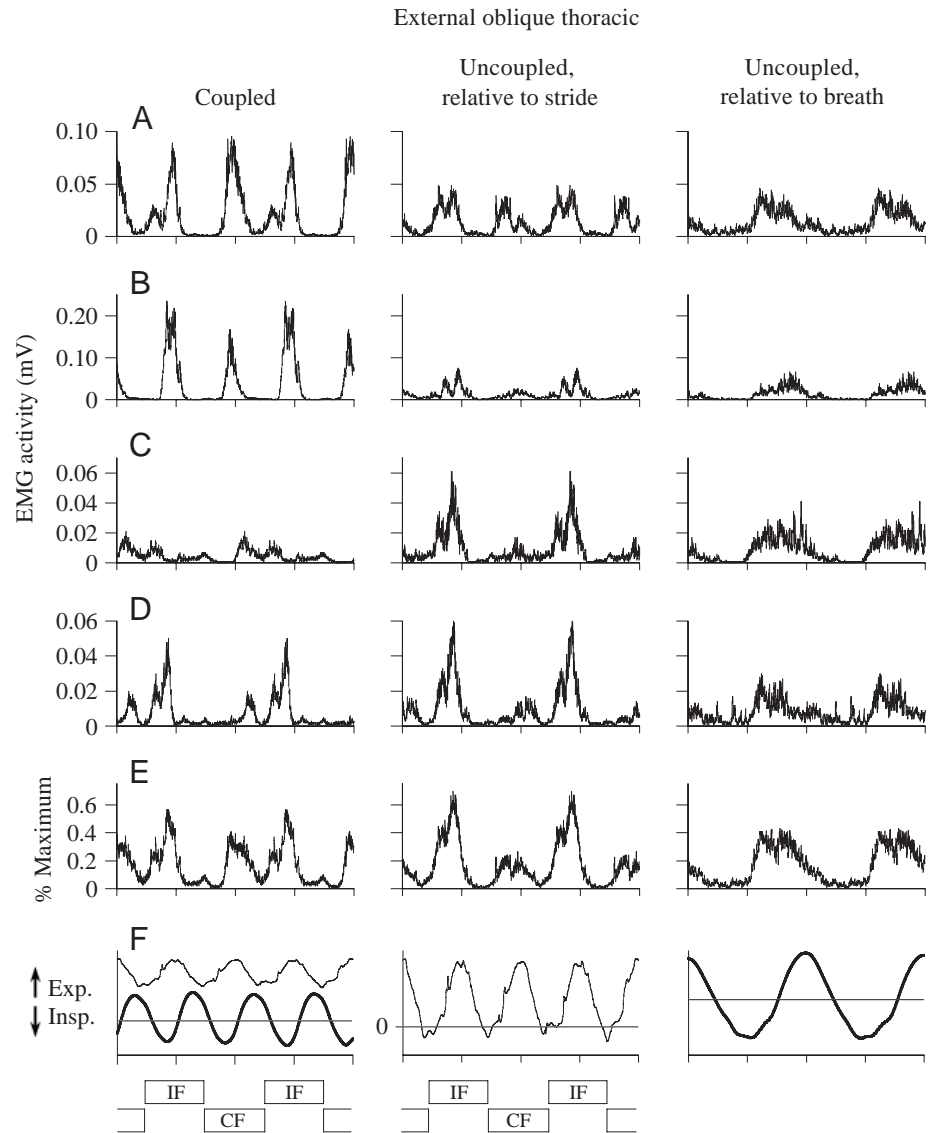

Fig. 6. Ensemble averages of electromyographic (EMG) activity of the thoracic portion of the external oblique muscle. This muscle clearly functions in both ventilation and locomotion, and the bursting pattern is consistent among dogs in both uncoupled stride and breath averages. Bursting starting at peak inspiratory airflow and extending to peak expiratory airflow reveals an expiratory function for this muscle. Samples are from four dogs (A–D), and the average across four dogs (E), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (F). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

occurred during the second half of inspiration, appropriate for expiration.

Transversus abdominis

The transversus abdominis muscle showed bursting in both uncoupled stride averages and breath averages. It was active during mid-forelimb support in both the coupled averages and the uncoupled stride averages (Fig. 9). Activity during ipsilateral forelimb support was slightly greater than activity during contralateral forelimb support, particularly in uncoupled stride averages. In uncoupled breath averages, a burst extended from peak inspiratory airflow to peak expiratory airflow, a pattern consistent with an expiratory function. During panting at rest (Fig. 2), this muscle was active during the second half of inspiration, also consistent with an expiratory function.

Deep pectoralis

The deep pectoralis muscle showed bursting in uncoupled stride averages and coupled averages and almost none in uncoupled breath averages (Fig. 10). Activity was associated with the latter half of contralateral forelimb support and early ipsilateral forelimb support. A very slight increase in activity was associated with inspiration in one dog, but the absence of any pattern during standing and panting (Fig. 2) indicates no ventilatory function for the deep pectoralis.

Longissimus dorsi

The longissimus dorsi muscle showed phasic activity in coupled averages and uncoupled stride averages (Fig. 11). A single burst occurred during the second half of contralateral forelimb support. Uncoupled breath averages showed no bursting or periodic increases in activity, indicating no ventilatory function for the longissimus dorsi. No activity was present during standing and panting (Fig. 2); thus, there is no ventilatory role for this muscle during rest.

Discussion

Muscle function

The hypaxial muscles examined in this study can be grouped as follows on the basis of the functional categories defined in Materials and methods. (i) Muscles with a pure locomotor function are the

deep pectoralis and longissimus dorsi. (ii) Muscles with a primarily locomotor function are the internal and external oblique abdominal muscles. (iii) Muscles with a dual function include the external intercostal, internal intercostal, external oblique thoracic and transversus abdominis. (iv) The only muscle with a solely ventilatory function is the parasternal portion of the internal intercostals.

The pectoralis and longissimus dorsi muscles appear to have a pure locomotor function during running. The high correlations between uncoupled versus coupled stride averages
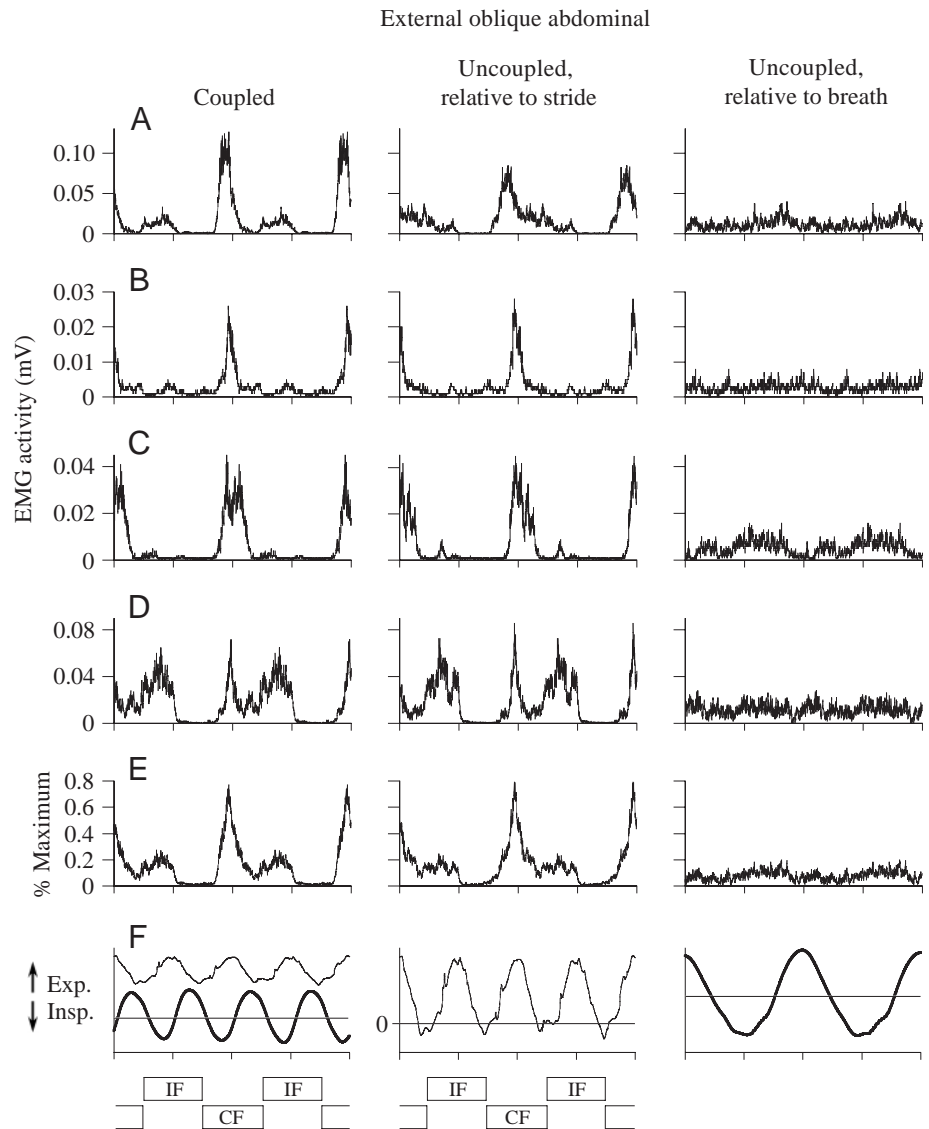

Fig. 7. Ensemble averages of electromyographic (EMG) activity of the abdominal portion of the external oblique muscle. This muscle has a locomotor function, revealed by a consistent bursting pattern in all dogs and a clear bursting pattern in the average across dogs. A ventilatory function is not evident, given the absence of bursting in the uncoupled breath averages. Samples are from four dogs (A–D), and the average across four dogs (E), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (F). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

(r^2=0.72 and r^2=0.96, respectively; Table 1) indicate that the locomotor functions of these muscles were relatively unaffected by whether breathing was coupled. The low correlations between breath averages (r^2=0.02 and r^2=0.003, respectively) reflect the absence of a ventilatory function for these muscles. The pectoralis and longissimus dorsi are appendicular and epaxial muscles, respectively, and showed no ventilatory activity during standing and panting, as expected for muscles in their positions. The longissimus dorsi muscle is in a position to extend the back or resist flexion, and it has been suggested that it helps to stabilize the trunk against inertial loading, which causes the trunk to sag and rebound during each trotting step (Ritter et al., 2001). The activity of this muscle during forelimb support is consistent with this hypothesized function. The pectoralis muscle is in a position to retract the forelimb or resist protraction (Evans, 1993), and its activity just prior to and during early ipsilateral forelimb support suggests that it breaks the forward movement of the forelimb and accelerates it backwards. The activity of the pectoralis ceases early in support, indicating that it does not contribute to forward propulsion.

The internal oblique abdominal and external oblique abdominal muscles had an expiratory function when the dogs were at rest, but abandoned this function during running, and their activity remained associated with locomotor events. The high correlations between uncoupled and coupled stride averages (r^2=0.88 for both; Table 1) indicate that their locomotor functions were relatively unaffected by whether breathing was coupled. The low correlations between breath averages (r^2=0.07 and r^2=0.14, respectively) indicate that these muscles abandon ventilatory function during trotting. A similar relationship has been observed in humans, in which these muscles contribute to expiration at rest (De Troyer and Loring, 1986) but adopt a postural function during appendicular movements (Hodges and Gandevia, 2000). In running birds, these muscles have been found to maintain a primarily locomotor function in some species and a ventilatory function in others (Nassar, 1994; Boggs et al., 1999).

The external intercostal, external oblique thoracic and transversus abdominis muscles have a dual function during trotting, providing postural support against the forces exerted on the trunk by the extrinsic appendicular muscles and generating changes in thoracic volume that power ventilation. These muscles also have a ventilatory function when the dogs are at rest (Fig. 2). Of these muscles, the external intercostal had the lowest correlation between stride ensemble averages (r^2=0.28; Table 1), indicating that its locomotor function is affected the most by uncoupled breathing. Conversely, only the transversus abdominis showed high correlations both between breath averages (r^2=0.83) and between stride averages (r^2=0.79), indicating that this muscle is capable of performing locomotor and ventilatory functions simultaneously, even if breathing is
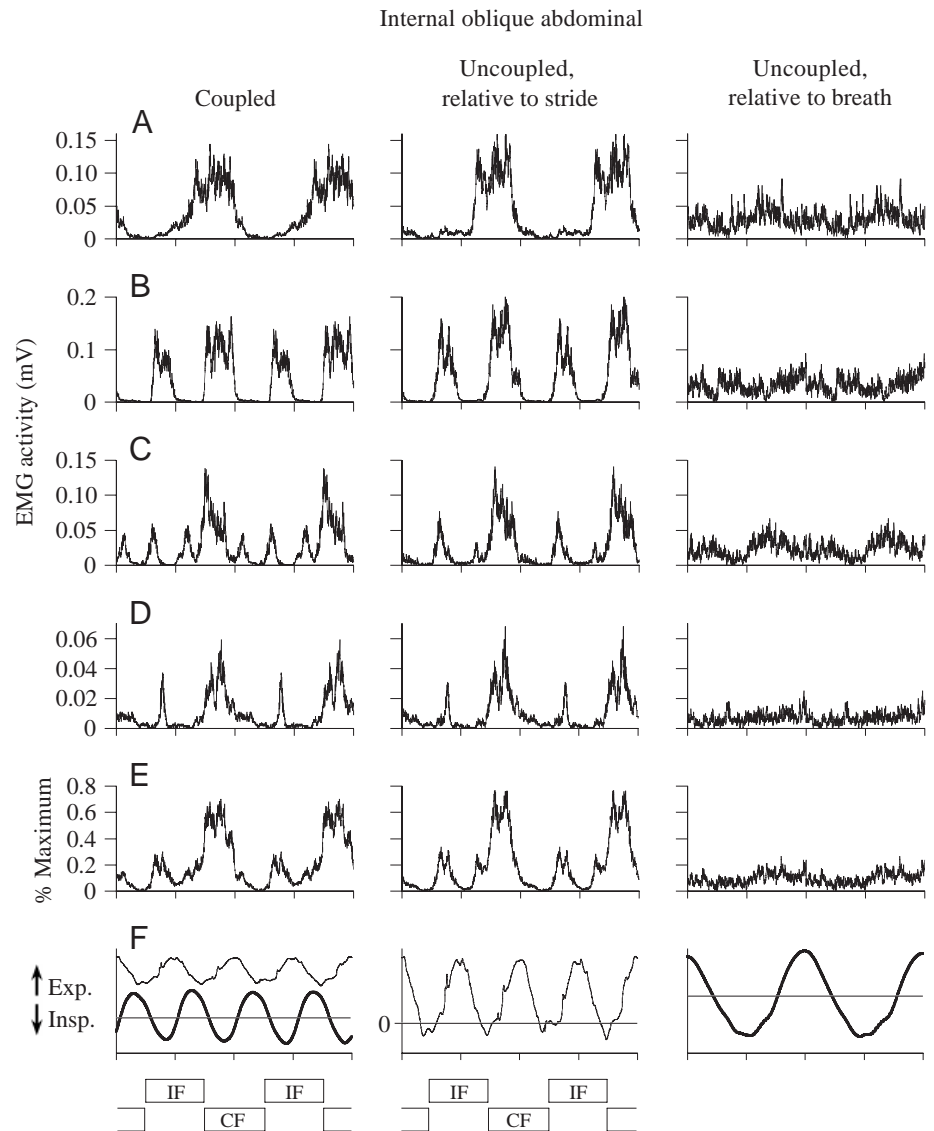

Fig. 8. Ensemble averages of electromyographic (EMG) activity of the abdominal portion of the internal oblique muscle. As in Fig. 7, this muscle has a locomotor function but no ventilatory function during running. Samples are from four dogs (A–D), and the average across four dogs (E), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (F). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

uncoupled. This dual ventilatory and postural role of the transversus abdominis has been observed previously in dogs (Ainsworth et al., 1996) and humans (Hodges and Gandevia, 2000). In humans, the transversus abdominis has separate populations of motor neurons for postural and ventilatory functions (Puckree et al., 1998). The dual-function muscles in general showed a clean bursting pattern in the coupled averages but a noisier bursting pattern in both uncoupled averages, indicating slight shifts in timing of bursts and, hence, some level of conflict between locomotor and ventilatory functions.

The internal intercostal muscle showed a similar pattern, but exhibited only slight bursting in the uncoupled breath average. Thus, it may be considered a muscle with a dual function, but with more of a locomotor role (or less of a ventilatory role) than the other dual-function muscles. Supporting this interpretation is the observation that the internal intercostal maintained the same clean bursting pattern in the coupled average and the uncoupled stride average, while the uncoupled breath average was much noisier, and the observation that the correlation between stride ensemble averages was high (r^2=0.83; Table 1). The low correlation between breath averages (r^2=0.06) is not due to an absence of bursting in the uncoupled breath average, as it is for the oblique abdominal muscles, but rather to a temporal redistribution of the bursts in the uncoupled breath average such that they do not match those in the coupled breath average.

The parasternal portion of the internal intercostal muscle showed the most unusual EMG pattern of all the muscles examined. We place it in the category of ventilatory muscles because it was active during inspiration while the dogs stood panting, as has been shown previously (DeTroyer and Loring, 1986), stayed synchronized with inspiration during both coupled and uncoupled breathing and had a higher correlation between breath averages (r^2=0.35; Table 1) than between stride averages (r^2=0.001). However, the relatively low correlation between breath averages reveals that uncoupled breathing disrupted the ventilatory function of this muscle to some extent. The average across all dogs (Fig. 5E) showed a noisy trace in the uncoupled stride average, but relatively clean bursts in the coupled average and the uncoupled breath average. Carrier (1996) found the same pattern in trotting dogs. The absence of a

consistent pattern of activity when averaged relative to locomotor events makes it impossible to assign a locomotor role to this muscle that would be the same in all dogs.

Dual role of the interosseus intercostal muscles

Carrier (1996) examined the EMG activity of the intercostal muscles of dogs during trotting and breathing and obtained similar results, but with an interesting difference from the results reported here: the internal and external intercostal muscles (interosseus portions) at two positions on the trunk showed bursting in the uncoupled stride average and no bursting in the
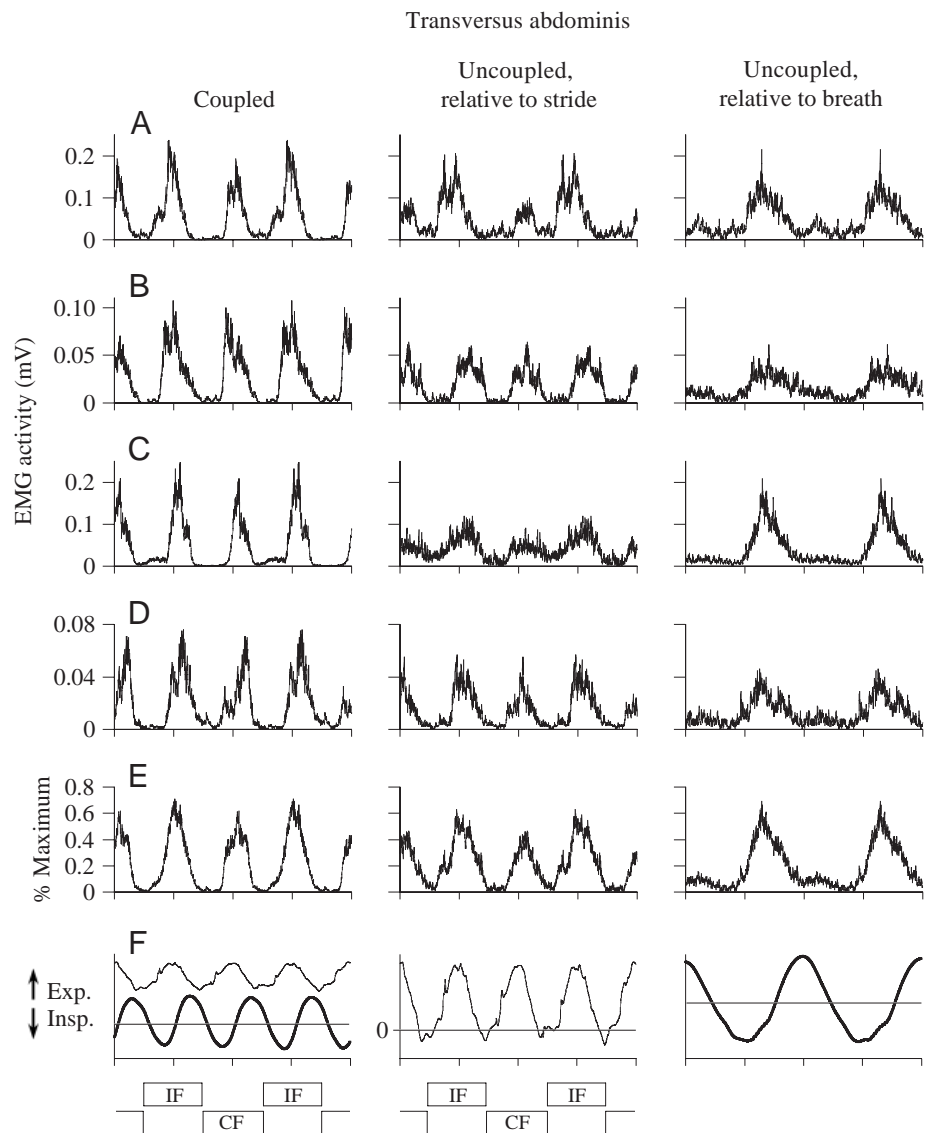

Fig. 9. Ensemble averages of electromyographic (EMG) activity of the transversus abdominis muscle. This muscle shows clear bursting in all ensemble averages, consistently across dogs, indicating both a ventilatory and locomotor function. The pattern of activity relative to the ventilatory cycle reveals an expiratory function for this muscle. Samples are from four dogs (A–D), and the average across four dogs (E), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (F). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

uncoupled breath average (compared with bursting in both uncoupled stride and uncoupled breath averages in the present study). The results of Carrier (1996) led to the conclusion that the intercostal muscles have a primarily locomotor function and abandon their ventilatory role in running dogs. We do not doubt the veracity of these results or conclusions, and think they can be reconciled with the current study by considering the different loads placed on the ventilatory system in the two different experiments. Carrier (1996) used a low-resistance mask-mounted screen pneumatachograph with a bias flow of $2–41s^{-1}$ to provide fresh air for respiration, which produced small negative pressures in the mask (–29.4 to –61.8 Pa; –0.30 to –0.63 cmH$_2$O). The current study used a tube-mounted screen pneumatachograph with a higher resistance to flow and consequently greater negative pressures (–55 to –164 Pa; –0.56 to –1.67 cmH$_2$O for $2–41s^{-1}$ airflow) in the mask. We suspect that this increased negative pressure in the current system (more than double the pressure of the previous system at higher flows) loaded the respiratory system and forced the dogs to work harder to breathe than in the earlier study.

The differences in the methods used and data from these two studies suggest that controlled studies in which respiratory load is changed would be worthwhile. These studies suggest that dogs are capable of recruiting the intercostal muscles, particularly the external intercostal, for both ventilation and locomotion when necessary, but are also capable of using the intercostal muscles solely for locomotion when the opportunity arises. In nature, circumstances must arise when the ventilatory system experiences differing locomotor loads, such as running uphill or carrying prey *versus* running unencumbered on level ground, and the respiratory system would need to make adjustments to muscular recruitment to counteract the loads. Similarly, recent work in sheep and dogs indicates that, in species that pant to thermoregulate and that couple their ventilation to the locomotor cycle during galloping, regulation of body temperature during galloping competes with control of pH balance (Entin et al., 1998, 1999; Wagner et al., 1997). Thus, an ability to modulate the recruitment of the intercostals muscles for locomotor or ventilatory function as the need arises during trotting would appear to be beneficial.

Implications for integration and neural control

The observation that dogs can ventilate their lungs using various combinations of hypaxial muscles while standing and panting (Fig. 2) suggests that there is functional overlap and even redundancy in the ventilatory musculature. This interpretation is supported by the observation discussed above that muscles, such as the intercostals, are recruited for breathing during trotting as ventilatory load changes. We propose that the functional redundancy of the ventilatory musculature may circumvent locomotor–ventilatory conflicts in particular muscles and allow dogs to maintain steady breathing under changing locomotor forces acting on the trunk and under changing ventilatory loads. Hence, both the functional redundancy of the hypaxial musculature and the dual role of some muscles in locomotion and ventilation indicate that the neural control of ventilation during running in mammals is more complex than is generally recognized.

A running mammal not only must adjust the activity of its ventilatory muscles to accomplish gas exchange, thermoregulation (Lee and Banzett, 1997) and to regulate acid–base balance (Entin et al., 1999), it must also change the activity of its ventilatory muscles in accordance with their locomotor functions. The examples mentioned above of running uphill or carrying prey not only increase metabolic rate, requiring
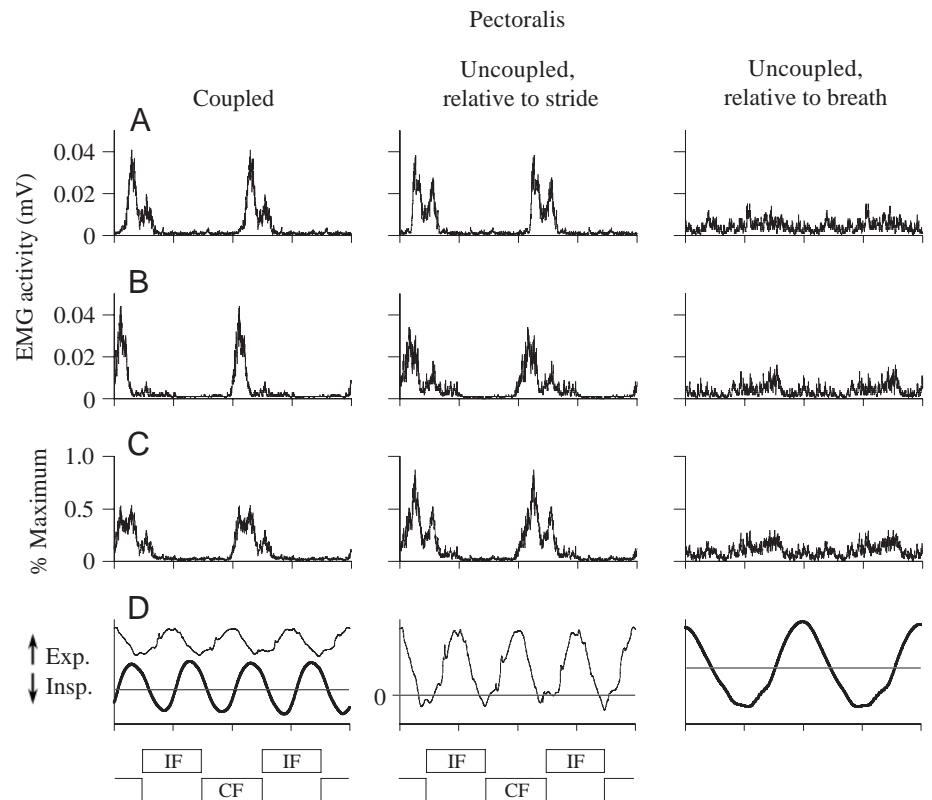

Fig. 10. Ensemble averages of electromyographic (EMG) activity of the deep pectoralis muscle. This muscle has a clear locomotor function that is consistent between dogs, but no ventilatory function. Samples are from two dogs (A and B), and the average across two dogs (C), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (D). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

greater rates of ventilation, but they also change the need for locomotor recruitment of the hypaxial muscles responsible for ventilation. Running uphill, for example, is associated with increased activity of the internal oblique and internal intercostal muscles in dogs, but decreased activity of the external oblique and external intercostal muscle (Fife et al., 2001). The pattern is reversed when dogs run downhill: greater activity in the external oblique and intercostal and less activity in the internal oblique and intercostal muscles. These adjustments in recruitment appear to stabilize the trunk against activity of the extrinsic appendicular muscles that place shearing forces on the trunk in the sagittal plane (Fife et al., 2001). Furthermore, in the variable terrain of the natural world, every step is different in the forces applied to the trunk and in the period of force application. Hence, every step would place variable and possibly unpredictable demands on the activity and force production of the hypaxial muscles responsible for lung ventilation. How the nervous system modifies the activity of the axial muscles during running to maintain the mechanical integrity of the trunk while at the same time adjusting ventilation in accordance with the need for gas exchange and thermoregulation remains difficult to imagine and largely unstudied.

The problem the nervous system faces in coordinating ventilation and locomotion using shared muscles might conceivably be simplified by coupling the two cycles in a limited number of possible phase relationships. The idea that coupling reduces mechanical conflicts and may thus improve the economy of ventilation is not new (Bramble and Carrier, 1983; Young et al., 1992; Bramble and Jenkins, 1993; Boggs et al., 1997; Boggs, 1997; Funk et al., 1997; Lee and Banzett, 1997; Entin et al., 1999; Nassar et al., 2001). In humans, although our locomotor and ventilatory functions are largely uncoupled because of our bipedality, coupling is routine in most experienced runners (Bramble and Carrier, 1983; Bramble, 1983), and running with coupled breathing appears to be slightly more economical than running with uncoupled breathing (Bernasconi and Kohl, 1993). An even greater energetic benefit of coupled breathing is expected in quadrupeds, in which the trunk plays a greater role in locomotion (Carrier, 1984).

Given the demands of locomotion on the trunk musculoskeletal system and the dual function of the hypaxial muscles in quadrupeds, specific periods in a trotting cycle may mechanically facilitate inspiration and other periods may

facilitate expiration. In addition, coupling locomotion and ventilation in particular phase relationships (2:1 or 1:1) may simplify the pattern of activation needed in the hypaxial musculature (Banzett et al., 1992a,b; Lee and Banzett, 1997) and may help the muscles to perform both functions simultaneously. This line of reasoning suggests that breathing in an uncoupled pattern would require greater muscular recruitment and more complicated neural control. Ventilatory–locomotor coupling is known to occur only in birds and mammals and thus is likely to have evolved independently (Carrier, 1987b), and in both mammals and running birds the resonant frequency of the respiratory system matches the natural frequency of the locomotor cycle (Young et al., 1992; Nassar et al., 2001). This convergent evolution suggests that coupling has a selective advantage. Reducing functional conflicts in the trunk musculature and simplifying control demands may have been selective forces contributing to the evolution of coupling.
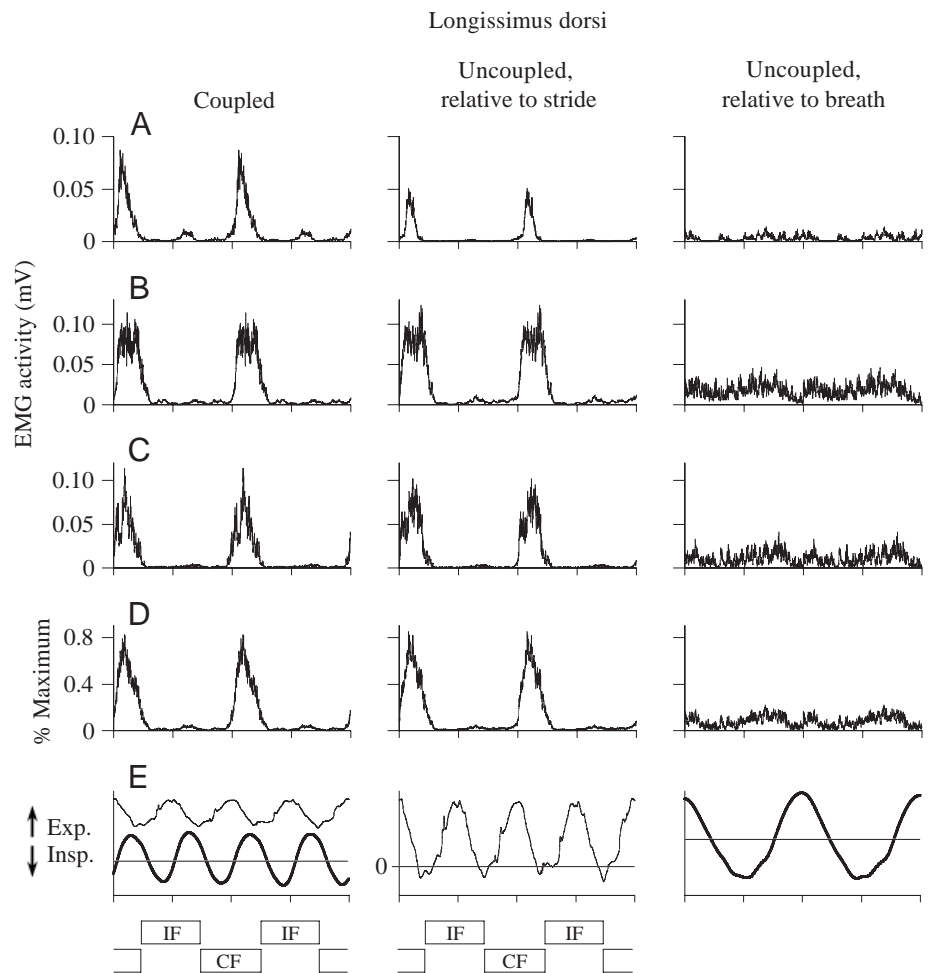

Fig. 11. Ensemble averages of electromyographic (EMG) activity of the longissimus dorsi, revealing a consistent locomotor function but no ventilatory function. Samples are from three dogs (A–C), and the average across three dogs (D), with ventilatory (bold lines) and acceleration (thin lines) traces to reveal relationships to breath and stride (E). IF indicates ipsilateral forelimb support and CF contralateral forelimb support in the footfall bars at the bottom. All traces are on the same time scale. Exp., expiration; Insp., inspiration.

References

Ainsworth, D. M., Smith, C. A., Henderson, K. S. and Dempsey, J. A. (1996). Breathing during exercise in dogs – passive or active? *J. Appl. Physiol.* **81**, 586–595.

Banzett, R. B., Mead, J., Reid, M. B. and Topulos, G. P. (1992a). Locomotion in men has no appreciable mechanical effect on breathing. *J. Appl. Physiol.* **72**, 1922–1926.

Banzett, R. B., Nations, C. S., Wang, N., Butler, J. P. and Lehr, J. L. (1992b). Mechanical independence of wingbeat and breathing in starlings. *Respir. Physiol.* **89**, 27–36.

Bennett, W. O., Simons, R. S. and Brainerd, E. L. (2001).Twisting and bending: the functional role of salamander lateral hypaxial musculature during locomotion. *J. Exp. Biol.* **204**, 1979–1989.

Berger, M., Roy, O. Z. and Hart, J. S. (1970). The co-ordination between respiration and wing beats in birds. *Z. Vergl. Physiol.* **66**, 190–200.

Bernasconi, P. and Kohl, J. (1993). Analysis of co-ordination between breathing and exercise rhythms in man. *J. Physiol., Lond.* **471**, 693–706.

Boggs, D. F. (1997). Coordinated control of respiratory pattern during locomotion in birds. *Am. Zool.* **37**, 41–57.

Boggs, D. F., Butler, P. J., Baudinette, R. V. and Frappell, P. B. (1999). Relationship amongst air sac pressures, steps and abdominal muscle activity in waddling and running birds. *FASEB J.* **13**, A495.

Boggs, D. F., Jenkins, F. A. and Dial, K. P. (1997). The effect of the wingbeat cycle on respiration in black-billed magpies (*Pica pica*). *J. Exp. Biol.* **200**, 1403–1412.

Brainerd, E. L. (1998). Mechanics of lung ventilation in a larval salamander *Ambystoma tigrinum*. *J. Exp. Biol.* **201**, 2891–2901.

Brainerd, E. L. (1999). New perspectives on the evolution of lung ventilation mechanisms in vertebrates. *Exp. Biol. Online* **4**, 11–28.

Brainerd, E. L. and Monroy, J. A. (1998). Mechanics of lung ventilation in a large aquatic salamander, *Siren lacertina*. *J. Exp. Biol.* **201**, 673–682.

Bramble, D. M. (1983). Respiratory patterns and control during unrestrained human running. In *Modeling and Control of Breathing* (ed. B. J. Whipp and D. M. Wiberg), pp. 213–220. New York: Elsevier.

Bramble, D. M. and Carrier, D. R. (1983). Running and breathing in mammals. *Science* **219**, 251–261.

Bramble, D. M. and Jenkins, F. A. (1989). Structural and functional integration across the reptile–mammal boundary: the locomotor system. In *Complex Organismal Functions: Integration and Evolution in Vertebrates* (ed. D. B. Wake and G. Roth), pp. 133–146. New York: John Wiley & Sons Ltd.

Bramble, D. M. and Jenkins, F. A. (1993). Mammalian locomotor–respiratory integration: implications for diaphragmatic and pulmonary design. *Science* **262**, 235–240.

Carrier, D. R. (1984). The energetic paradox of human running and hominid evolution. *Curr. Anthropol.* **25**, 483–495.

Carrier, D. R. (1987a). Lung ventilation during walking and running in four species of lizards. *J. Exp. Biol.* **47**, 33–42.

Carrier, D. R. (1987b). The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. *Paleobiology* **13**, 326–341.

Carrier, D. R. (1989). Ventilatory action of the hypaxial muscles of the lizard *Iguana iguana*: a function of slow muscle. *J. Exp. Biol.* **143**, 435–457.

Carrier, D. R. (1990). Activity of the hypaxial muscles during walking in the lizard *Iguana iguana*. *J. Exp. Biol.* **152**, 453–470.

Carrier, D. R. (1991). Conflict in the hypaxial musculo-skeletal system: documenting an evolutionary constraint. *Am. Zool.* **31**, 644–654.

Carrier, D. R. (1993). Action of the hypaxial muscles during walking and swimming in the salamander, *Dicamptodon ensatus*. *J. Exp. Biol.* **180**, 75–83.

Carrier, D. R. (1996). Function of the intercostal muscles in trotting dogs: ventilation or locomotion? *J. Exp. Biol.* **199**, 1455–1465.

Davis, J. R. and Mirka, G. A. (2000). Transverse-contour modeling of trunk muscle-distributed forces and spinal loads during lifting and twisting. *Spine* **25**, 180–189.

De Troyer, A. and Loring, S. H. (1986). Action of the respiratory muscles. In *Handbook of Physiology, The Respiratory System* (ed. P. T. Macklem and J. Mead), pp. 443–561. Bethesda, MD: American Physiological Society.

Entin, P. L., Robertshaw, D. and Rawson, R. E. (1998). Thermal drive contributes to hyperventilation during exercise in sheep. *J. Appl. Physiol.* **85**, 318–325.

Entin, P. L., Robertshaw, D. and Rawson, R. E. (1999). Effect of locomotor respiratory coupling on respiratory evaporative heat loss in the sheep. *J. Appl. Physiol.* **87**, 1887–1893.

Evans, H. E. (1993). *Miller's Anatomy of the Dog.* Third edition. Philadelphia: W. B. Saunders Company.

Farley, B. G. and Koshland, G. F. (2000). Trunk muscle activity during the simultaneous performance of two motor tasks. *Exp. Brain Res.* **135**, 483–496.

Fife, M. M., Bailey, C., Lee, D. V. and Carrier, D. R. (2001). Function of the oblique hypaxial muscles in trotting dogs. *J. Exp. Biol.* **204**, 2371–2381.

Funk, G. D., Valenzuela, I. J. and Milsom, W. K. (1997). Energetic consequences of coordination wingbeat and respiratory rhythms in birds. *J. Exp. Biol.* **200**, 915–920.

Gardner-Morse, M. G. and Stokes, I. A. F. (1998). The effects of abdominal muscle coactivation on lumbar spine stability. *Spine* **23**, 86–92.

Hodges, P. W. and Gandevia, S. C. (2000). Changes in intra-abdominal pressure during postural and respiratory activation of the human diaphragm. *J. Appl. Physiol.* **89**, 967–976.

Hodges, P. W., Gandevia, S. C. and Richardson, C. A. (1997). Contractions of specific abdominal muscles in postural tasks are affected by respiratory maneuvers. *J. Appl. Physiol.* **83**, 753–760.

Lee, H.-T. and Banzett, R. B. (1997). Mechanical links between locomotion and breathing: can you breathe with your legs? *News Physiol. Sci.* **12**, 273–278.

Liem, K. F. (1985). Ventilation. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 185–209. Cambridge, MA: Harvard University Press.

Loeb, G. E. and Gans, C. (1986). *Electromyography for Experimentalists.* Chicago, IL: University of Chicago Press.

McGill, S. M. (1991). Electromyographic activity of the abdominal and low back musculature during the generation of isometric and dynamic axial trunk torque: implications for lumbar mechanics. *J. Orthop. Res.* **9**, 91–103.

Morris, J. M., Lucas, D. B. and Bresler, M. S. (1961). Role of the trunk in stability of the spine. *J. Bone Joint Surg.* **43**, 327–351.

Nassar, P. N. (1994). A dual role for the abdominal muscles of running birds. *Am. Zool.* **34**, 15A.

Nassar, P., Jackson, A. and Carrier, D. R. (2001). Entraining the natural frequencies of running and breathing in guinea fowl. *J. Exp. Biol.* **204**, 1641–1651.

Owerkowicz, T., Farmer, C. G., Hicks, J. W. and Brainerd, E. L. (1999). Contribution of gular pumping to lung ventilation in monitor lizards. *Science* **284**, 1661–1663.

Puckree, T., Cerny, F. and Bishop, B. (1998). Abdominal motor unit activity during respiratory and nonrespiratory tasks. *J. Appl. Physiol.* **84**, 1707–1715.

Ritter, D. (1995). Epaxial muscle function during locomotion in a lizard (*Varanus salvator*) and the proposal of a key innovation in the vertebrate axial musculoskeletal system. *J. Exp. Biol.* **198**, 2477–2490.

Ritter, D. (1996). Axial muscle function during lizard locomotion. *J. Exp. Biol.* **199**, 2499–2510.

Ritter, D., Nassar, P., Fife, M. and Carrier, D. R. (2001). Function of the epaxial muscles in trotting dogs. *J. Exp. Biol.* **204**, 3053–3064.

Simons, R. S., Bennett, W. O. and Brainerd, E. L. (2000). Mechanics of lung ventilation in a post-metamorphic salamander, *Ambystoma tigrinum*. *J. Exp. Biol.* **203**, 1081–1092.

Wagner, J. A., Horvath, S. M. and Dahms, T. E. (1997). Cardiovascular, respiratory and metabolic adjustments to exercise in dogs. *J. Appl. Physiol.* **42**, 403–407.

Wang, T., Carrier, D. R. and Hicks, J. W. (1997). Ventilation and gas exchange in lizards during treadmill exercise. *J. Exp. Biol.* **200**, 2629–2639.

Young, I. S., Warren, R. D. and Altringham, J. D. (1992). Some properties of the mammalian locomotory and respiratory systems in relation to body mass. *J. Exp. Biol.* **164**, 283–294.

Zetterberg, C., Andersson, G. B. J. and Schultz, A. B. (1987). The activity of individual trunk muscles during heavy physical loading. *Spine* **12**, 1035–1040.