ACTIVITY OF THE HYPAXIAL MUSCLES DURING WALKING IN THE LIZARD *IGUANA IGUANA*

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Summary

The role that the hypaxial muscles play in locomotion has been largely ignored by biologists. In tetrapods, there are at least three possibilities. First, the hypaxial muscles might bend the trunk laterally to increase stride length. Second, they might stabilize the trunk against the horizontal, lateral and vertical components of the propulsive force. Alternatively, they might not be involved in locomotion. This study evaluated these three hypotheses by analyzing the activity of the hypaxial muscles of green iguanas (*Iguana iguana*). During walking, the rectus abdominis, obliquus externus superficialis and profundus, intercostales externi, and ventral portion of the intercostales interni on one side of the trunk acted synergistically with the lateral portion of the intercostales interni and obliquus internus on the other side of the trunk. This pattern supports the hypothesis that the hypaxial muscles act to stabilize the trunk during locomotion. Specifically, the longitudinally oriented rectus abdominis, obliquus externus profundus and ventral portion of the intercostales interni appear to stabilize the trunk against the horizontal and lateral components of the propulsive force, which tend to rotate the girdles in the horizontal plane. The obliquely oriented obliquus externus superficialis, intercostales externi, lateral portion of the intercostales interni and obliquus internus appear to stabilize the trunk against the vertical component, which induces long-axis torsion in the trunk. Thus, the demands of locomotion may provide a functional explanation for the basic organization of the hypaxial muscles of tetrapods.

Introduction

The hypaxial muscles have remained remarkably unchanged throughout the course of tetrapod evolution. Not only are these muscles organized in basically the same way in all limbed tetrapods, but aspects of this organization are also characteristic of bony fishes (Maurer, 1913). As in tetrapods, both teleosts and lungfish have two hypaxial muscles with opposing radial orientations (external and internal oblique) and a ventrally located longitudinal muscle (rectus abdominis) (Maurer, 1913). The broadly conservative nature of these muscles raises questions of function. For instance, why are such similar muscles found in animals that are as different as bony fishes and tetrapods?

Key words: hypaxial muscles, locomotion, tetrapod.

Biologists have paid relatively little attention to the functional significance of the hypaxial muscles. These muscles traditionally have been thought to support and compress the viscera of the abdominal cavity (Hildebrand, 1974; Radinsky, 1979). The diverse orientations of the different muscle layers have also been suggested to strengthen the body wall in a fashion analogous to the laminated construction of plywood (Romer and Parsons, 1977). However, the hypaxial muscles are most often considered to function in lung ventilation. This is appropriate given that some portion of the hypaxial musculature is critical to lung ventilation in all amniotes (Gesell, 1936; Fedde et al. 1964; Gaunt and Gans, 1969; Gans and Clark, 1976; Carrier, 1989). In spite of their clear role in breathing, mounting evidence suggests that lung ventilation alone cannot be used to explain the basic organization of these muscles (De Troyer et al. 1985; Carrier, 1989). One potential function of the hypaxial muscles which only recently has begun to attract interest is locomotion. The locomotor role of the hypaxial muscles has not been adequately addressed in any tetrapod. Indeed, there is very little evidence to indicate whether these muscles are or are not involved in locomotion.

There are at least three possible roles that the hypaxial muscles might play in locomotion. First, the hypaxial musculature might function to bend the trunk laterally to increase stride length. Marked lateral bending of the trunk characterizes the locomotion of most ectothermic tetrapods and commonly is suggested to increase stride length. If the hypaxial muscles did produce these movements, they probably would be active first on one side of the trunk and then on the other, to bend the body from side to side. Second, the hypaxial muscles might act to stabilize the trunk against the horizontal, lateral and vertical components of the propulsive force in a manner that allows the animal to progress in a controlled fashion. Because the limbs are displaced laterally from the centre of gravity, they exert moments which tend to bend and twist the axial skeleton (Gray, 1968). For a tetrapod to move forward, and also have flexibility in its movements, these forces must be resisted with muscles, rather than bones or ligaments. If the hypaxial muscles were to accomplish this, obliquely oriented muscles with opposite orientations on the two sides of the body would have to be active simultaneously. That is, the external oblique would be expected to be active on one side, while at the same time the internal oblique on the other side would be active. Third, it is possible that the hypaxial muscles may have little or nothing to do with locomotion. Locomotor movements of the trunk and stabilization of the trunk might result solely from the dorsal epaxial muscles. If this were true the hypaxial muscles would be inactive or active independently of the locomotor rhythm. In this study, I used electromyography to evaluate these three hypotheses in green iguanas.

Materials and methods

Experiments were performed on eight green iguanas (*Iguana iguana* Linnaeus, 500–2320 g). They were housed in large cat cages with a photothermal gradient

on a 12 h:12 h light:dark photoperiod, and were fed a diet of Romaine lettuce and Skippies dog food.

The hypaxial muscles were described from dissection of one specimen loaned by the Museum of Natural History, University of Kansas, and five specimens donated by the Smithsonian Tropical Research Institute.

Gait analysis

To correlate the pattern of limb support during walking with that of lateral bending of the trunk, three iguanas were video-taped from above, at 60 images per second, while they walked on a solid track. Simultaneous recordings were made of the bending of the trunk with a mercury strain gauge (Parks Electronics Laboratory, Aloha, Oregon) that was mounted on the skin of the back, parallel and lateral to the mid-line. The video-tape and chart recordings of the trunk bending were synchronized with a manual circuit that lit a light in the field of view of the camera and sent a d.c. pulse to the chart recorder. The video recordings were analyzed to determine the times at which each foot contacted the track surface and then lifted off again.

Electromyography

To induce deep anaesthesia, lizards were initially given intramuscular injections of 140 mg of ketamine per kilogram body mass, followed by one-third the initial dosage, as needed. Because the hypaxial muscles are a series of overlapping thin sheets, standard barbed bipolar electrodes are difficult to secure in individual muscles and are likely to receive signals from adjacent layers as well as the one they are intended to record from. To diminish both of these problems, patch electrodes were used in all experiments. Patch electrodes can be positioned and held in place between muscle layers that are much too thin to contain standard barbed bipolar electrodes. They also provide electrical insulation on one side, which greatly reduces the potential for cross-talk from muscles on that side (Loeb and Gans, 1986). Patches were constructed so that the bared electrodes were approximately 1.0 mm long and spaced 1.0 mm apart on a 5–10 mm square of Dow Corning 501-1 Silastic reinforced sheeting. Electrode wire was 75 μm diameter stainless-steel with Teflon insulation. Electrode wires passed percutaneously to exit points along the mid-line of the back. At the exit points the wires were glued to the skin and soldered to gold connector pins. Electrodes were connected to the preamplifiers *via* 10 m lightweight, shielded cables (NMUF 2/32–6550SJ, Cooner Wire Co., Chatsworth, CA). The electrical signals from the muscles were passed to Tektronix FM 122 preamplifiers, amplified 1000 times and filtered below 8 Hz and above 10 kHz. Signals were then amplified an additional 10 times by a set of a.c. amplifiers, and simultaneously stored on a Crown International 700 tape recorder and printed out on a Beckman R611 chart recorder.

After recovery from anaesthesia the lizards were tested on a 5 m long solid track. The lizards were allowed to choose the speed at which they walked. In all trials, lateral bending of the trunk was recorded (as described above) simul-

taneously with electromyograms from 3–4 electrodes. After completion of recording (generally 2–4 days) the lizards were anaesthetized again and the positions of the electrodes verified during their removal.

Electrode placement and cross-talk

Patch electrodes were implanted so as to record selectively from individual muscles. Sites of electrode placement are listed in Table 1. The possibility of cross-talk was eliminated for half the muscles by judicious placement of the electrodes. To verify that electrodes recording from the medial surface of the external intercostal were not receiving signals from the external oblique, trials were run in which Silastic sheeting was placed between the external oblique and the external intercostal (see Loeb and Gans, 1986; Mangun *et al.* 1986). This effectively shielded the electrodes on the external intercostal from any signals originating in the external oblique, and demonstrated that cross-talk was not present in the standard recordings from external intercostal muscle. To verify that signals received from the internal intercostal and internal oblique really did originate in

Table 1. *The numbers of specimens and electrodes from which electromyographic signals were recorded, muscle surface on which electrodes were placed and the potential sources of cross-talk for each of the muscles studied*

Muscle	Specimens/ Electrodes	Electrode placement	Source of cross-talk
External oblique superficial	3/7	Medial	None
External oblique deep	3/3	Medial	External oblique superficial
External intercostal	3/6	Medial	External oblique
Internal intercostal lateral	3/7	Lateral Medial	Internal oblique External intercostal
Internal intercostal ventral	2/4	Lateral	Internal oblique
Internal oblique	3/5	Lateral Medial	Transversalis External oblique
Transversalis	2/2	Lateral	None
Rectus abdominis	2/5	Lateral	None
Retrahentes costarum	2/4	Lateral	None
Pubic abdominis	2/3	Lateral	None

these two muscles, electrodes were placed on both surfaces of the muscles. Patch electrodes placed on opposite surfaces of a sheet-like muscle face opposite directions, and, therefore, have different potential sources of cross-talk. Consequently, recording the same pattern of activity from electrodes facing opposite directions strongly suggests that the recorded activity does originate in the muscle of interest and is not due to cross-talk. This procedure demonstrated that signals recorded from the internal intercostal and internal oblique were due to their own activity.

Results

Anatomy of the hypaxial musculature

The anatomy of the hypaxial musculo-skeletal system of *Iguana iguana* is described elsewhere (Carrier, 1988). Only those muscles analyzed in this investigation are described here.

Rectus abdominis

The rectus abdominis (*ra*) is a large superficial, segmented sheet that occupies the ventral and ventro-lateral abdominal region between the pelvic girdle and the pectoralis complex (Fig. 1A, E). It arises from a strong tendon that attaches along the length of the ventral aspect of the symphysis of the ischia, and can be divided into medial and lateral subunits that are differentiated by the attachment site of the internal oblique and transversalis muscles. The medial portion (i.e. medial to the attachment site of the internal oblique and transversalis) runs forward along the mid-line of the belly to insert on the last two costal cartilages and the posterior margin of the pectoralis complex. The lateral portion (i.e. lateral to the attachment site of the internal oblique and transversalis) is slightly thicker. It is continuous with the ventral component, but fans laterally and dorsally to occupy a position that is distinctly visible in lateral view. In contrast to the ventral portion, it does not insert on costal cartilages but attaches solely to the posterior margin of the pectoralis complex. The lateral portion serves as the site of origin for much of the external oblique muscles. The medial portion serves as a site of insertion of the pubic abdominis muscle and site of origin for the abdominal portions of the internal oblique and transversalis muscles.

Obliquus externus

The external oblique is the superficial muscle on the lateral aspect of the trunk (Fig. 1A). It is composed of two separate muscular sheets with fibres oriented anteriorly and dorsally. The superficial layer (obliquus externus superficialis; *oes*) is a thin sheet that originates on the spine of the pubis and the dorsal edge of the rectus abdominis. In the abdominal region the superficialis runs anteriorly and dorsally to insert on the aponeurosis of the transverse septum. In the thoracic region it inserts, *via* separate tendinous sheets, on the vertebral portion of each thoracic rib. The deep layer (obliquus externus profundus; *oep*) also has both
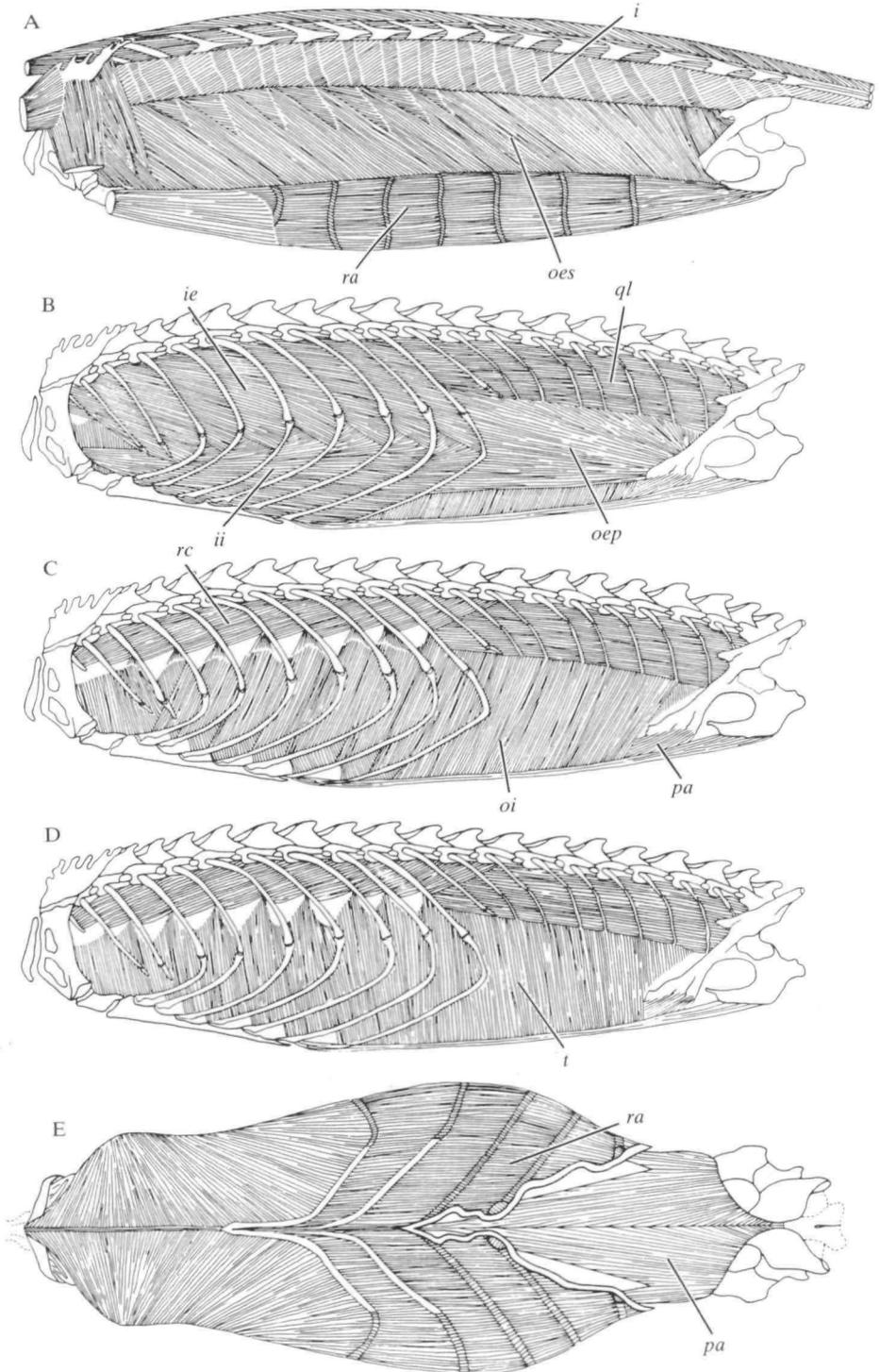
Fig. 1

abdominal and thoracic portions. The abdominal portion of the profundus originates on the spine of the pubis and courses anteriorly and dorsally to insert on the aponeurosis of the transverse septum and the last sternal rib (Fig. 1B). The thoracic portion of the profundus is thin and composed of semi-distinct slips directed to each of the thoracic ribs. Its origin is on the rectus abdominis, medial and ventral to that of the superficial layer. It inserts on the same tendinous sheets as the superficialis.

Intercostales externi

The external intercostal (*ie*) runs from rib to rib along the dorsolateral portion of the thorax (Fig. 1B). The muscle extends from the vertebral centra to just below the bend in the costal cartilages. Fibres run anteriorly and dorsally at an angle of 30–40° from the horizontal. The muscle becomes progressively thinner ventrally. Its dorsal half consists of two distinct layers with similar fibre angles.

Intercostales interni

The internal intercostal (*ii*) lies medial to the external intercostal and occupies a more ventral position in the thorax (Fig. 1B). The muscle extends, dorsoventrally, from the mid-portion of the vertebral ribs to the ventral aspect of the costal cartilages. Fibres making up the sheet above the bend in the costal cartilages are oriented at an angle of about 60° to the horizontal. Fibres below the bend have a largely longitudinal orientation. Thus, based on fibre orientation, the internal intercostal consists of lateral (*iil*) and ventral (*iiv*) portions. Posterior to the last thoracic rib, a slip of this muscle (i.e. retractor costae; not figured) extends dorsally to attach to the lumbo-dorsal fascia.

Obliquus internus

The internal oblique (*oi*) lies deep to the abdominal portion of the external intercostal in the abdominal region and deep to the internal intercostal in the thoracic region (Fig. 1C). The abdominal and thoracic portions have different sites of attachment. In the abdominal region, the internal oblique originates on the lumbo-dorsal fascia and inserts on the ventral portion of the rectus abdominis. In the thoracic region, the internal oblique originates on the mid-portion of the vertebral ribs and inserts on the mid-portion of the costal cartilages. The fibres of both abdominal and thoracic portions course anterio-ventrally at an angle of about 45°.

Fig. 1. Trunk musculature of *Iguana iguana*. (A) Lateral view of the superficial muscles. (B–D) Lateral views showing successively deeper hypaxial muscles. (E) Ventral view with the rectus abdominis cut away to show the pubic abdominis. *i*, iliocostalis; *ie*, intercostales externi; *ii*, intercostales interni; *oep*, obliquus externus profundus; *oes*, obliquus externus superficialis; *oi*, obliquus internus; *pa*, pubic abdominis; *ql*, quadratus lumborum; *ra*, rectus abdominis; *rc*, retrahentes costarum; *t*, transversalis.

Transversalis

The transversalis (t) is the innermost muscular sheet of the lateral body wall (Fig. 1D). It is quite thin, but continuous from girdle to girdle, with fibres oriented in a ventral and slightly posterior direction. The abdominal and thoracic portions have different sites of attachment. The transversalis abdominis originates on the lumbo-dorsal fascia and inserts on the dorsal aspect of the rectus abdominis. The transversalis thoracis originates on the mid-portion of the vertebral ribs, *via* tendinous sheets, and inserts on the lower part of the costal cartilages. As is the case for the internal oblique, the thoracic portion of the transversalis is entirely costal in its sites of origin and insertion.

Retrahentes costarum

The retrahentes costarum (rc) is confined to the dorsal thoracic region, deep to the intercostal musculature (Fig. 1C). Fibres originate on the ventral aspect of the centra of dorsal vertebrae 3–13 and course anterio-ventrally to insert on the mid-portion of the vertebral elements of ribs 2–11.

Pubic abdominis

The pubic abdominis (pa; rectus internus, Hoffman, 1866; Nishi, 1938) is a large fan-shaped muscle that lies deep to the rectus abdominis (Fig. 1E). It originates on the tuberosity of the pubis and fans medially and anteriorly to insert on the linea alba, rectus abdominis and posterior portion of the lesser omentum. It is slightly thicker than the rectus abdominis and can be separated into three heads. The lateral two insert on the second and third myosepta of the rectus abdominis and the third head inserts on the linea alba and lesser omentum.

Gait and trunk bending

Green iguanas walk by swinging the forelimb and hindlimb on opposite sides of the body in unison (Fig. 2). The three individuals that were analyzed exhibited the same pattern. As iguanas walk, their trunks bend laterally from side to side forming standing waves, with the nodes at the girdles. Limb support is tightly synchronized with these trunk movements. The hind foot contacts the ground 36 ± 41 ms (mean$\pm$s.D. $N=24$) before the trunk begins to bend laterally towards the contralateral side. For example, as the right hind foot contacts the ground the curvature of the trunk is concave to the right and it begins to straighten by extending to the left. Right hind support continues as the trunk flexes laterally to the left and ends 203 ± 144 ms ($N=24$) after the trunk reaches maximum flexion. The pattern of limb support and trunk bending is similar during running. The gait remains a trot, but the contact duration of the feet becomes a smaller portion of the locomotor cycle. In the run, as in the walk, contact of the hind foot begins shortly before the trunk starts to bend laterally to the contralateral side (6 ± 19 ms, $N=10$). However, hind support represents a relatively shorter portion of the locomotor cycle in the run, ending 9.7 ± 17 ms before the trunk reverses direction.

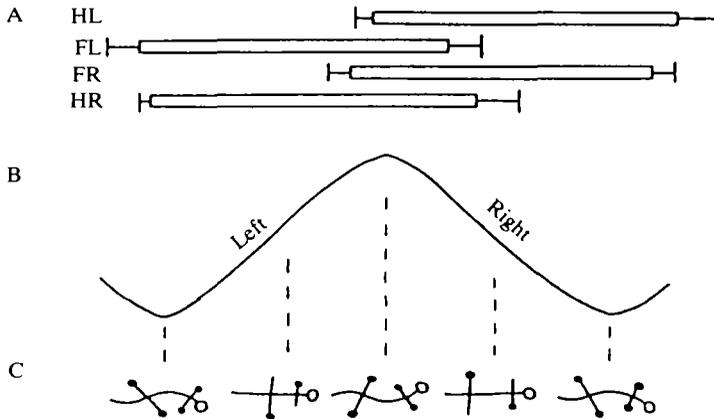The tight coupling between trunk bending and limb support makes it possible to

Fig. 2. Relationship between foot support and lateral trunk bending during walking in a green iguana *Iguana iguana*. (A) Mean and standard deviation of foot support plotted relative to lateral trunk bending ($N=14$ strides, stride frequency=$0.94\pm$ 0.25 strides s^{-1}). HL, left hind support; FL, left fore support; FR, right fore support; HR, right hind support. (B) Recording of trunk bending from mercury strain gauge on right side of trunk. Rise in trace indicates lateral bending to the left and drop in trace indicates lateral bending to the right. (C) Schematic representation of trunk bending and foot support. Solid circles represent feet in contact with the ground.

correlate muscle activity with limb support by recording trunk bending. Because trunk bending is more easily monitored than foot contact, muscle activity was recorded with reference to trunk bending.

Muscle activity

Electromyographic activity in the hypaxial muscles was stereotypic during walking (Fig. 3). Of the 10 muscles investigated, only the retrahentes costarum showed any ambiguity in activity pattern during walking locomotion. Table 1 lists the number of specimens and electrodes from which recordings were made from each muscle. Activity in eight of the muscles was correlated with the two phases of lateral bending of the trunk (Fig. 4). In these eight muscles, activity began as the trunk became maximally flexed or slightly before maximum flexion, and continued through bending to the opposite side. Activity ended at roughly the time the trunk was maximally flexed in the other direction. Thus, each of these muscles was active for approximately 50 % of the locomotor cycle.

Muscles with a longitudinal orientation (*ra, oep, iiv*) or anterio-dorsal oblique orientation (*oes, ie*) were active as the trunk extended (i.e. straightened) contralateral to the active muscle and as the trunk flexed ipsilateral to the active muscle (Fig. 4). In contrast, muscles with an anterio-ventral oblique orientation (*iil, oi*) were active during ipsilateral extension and contralateral flexion. Thus, during walking the rectus abdominis, superficial and deep layers of the external oblique, external intercostal and ventral portion of the internal intercostal on one
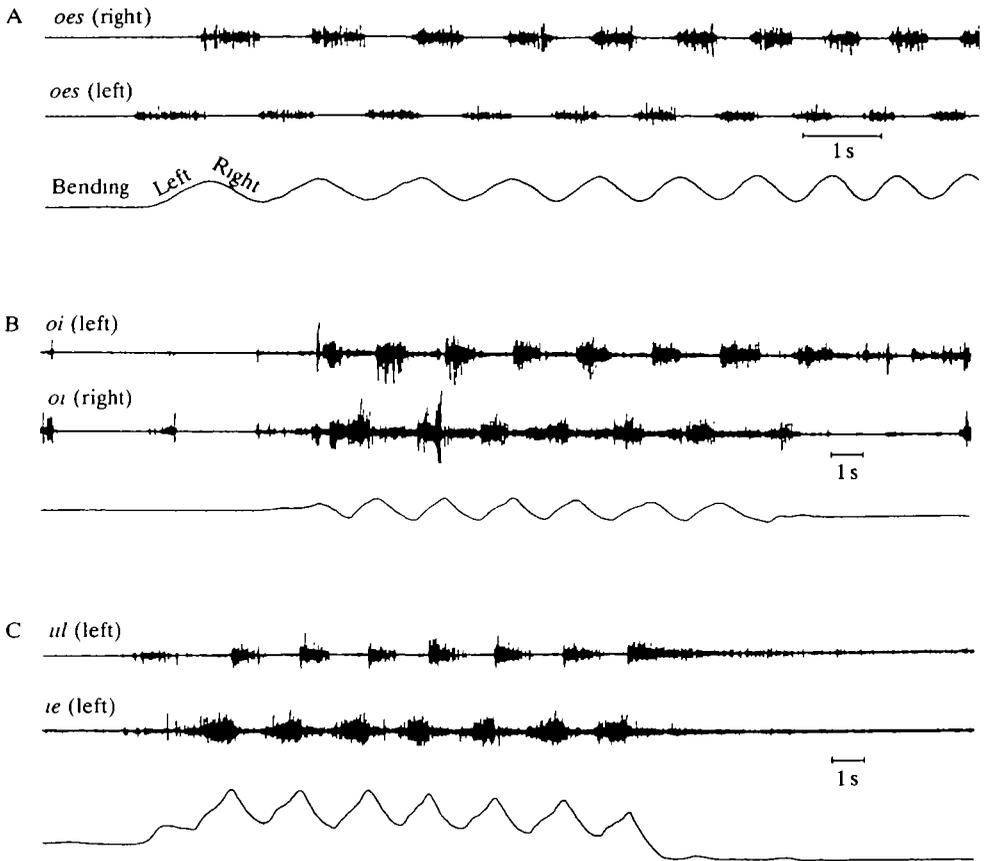
Fig. 3. Sample electromyographic recordings from the hypaxial muscles of *Iguana iguana* during walking. (A) Activity of the m. obliquus externus superficialis (*oes*) from the right and left sides of the trunk. Electrodes were positioned in the posterior abdominal region. The third trace is a recording of lateral bending of the trunk. (B) Activity of the m. obliquus internus (*oi*) from the left and right sides of the trunk. Electrodes were medial to the second sternal ribs. (C) Activity of the lateral portion of the m. intercostales interni (*iil*) and the m. intercostales externi (*ie*). Both electrodes were on the left side of the trunk, between ribs two and three.

side of the trunk acted synergistically with the lateral portion of the internal intercostal and internal oblique on the other side of the trunk.

The internal intercostal muscle has two regions with different fibre orientations. These two regions were active during opposite phases of the locomotor cycle (Fig. 5). The lateral portion of the internal intercostal, which has an anterioventral oblique orientation, was active during ipsilateral extension and contralateral flexion. The ventral portion, which has a longitudinal orientation, was active during contralateral extension and ipsilateral flexion.

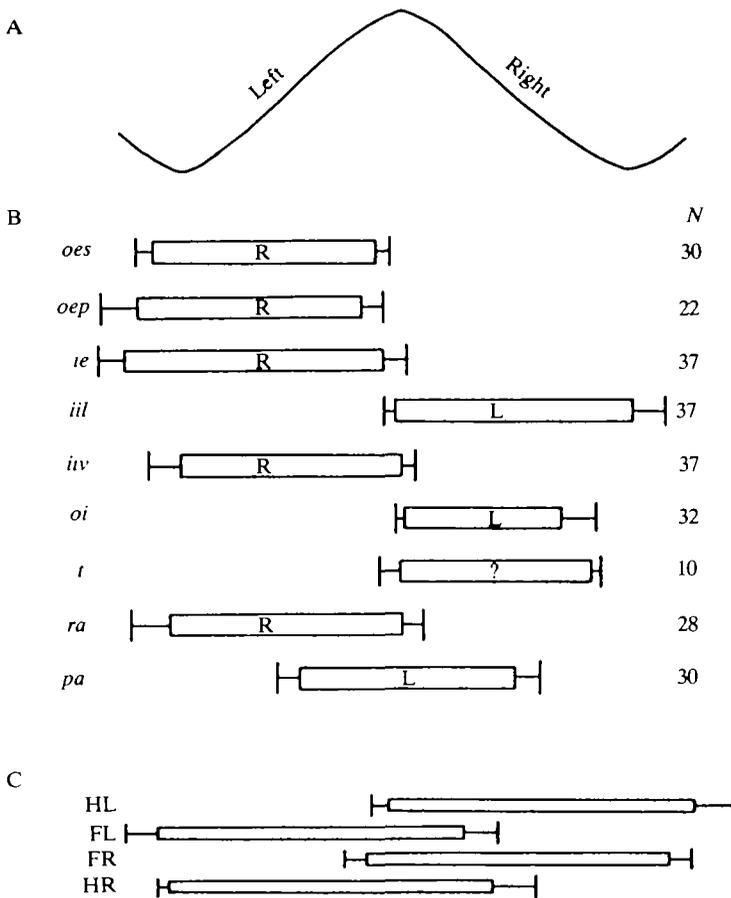Two of the hypaxial muscles displayed activity that differed from the pattern

Fig. 4. Onset and offset times of the hypaxial muscles on the left side of the body during walking in *Iguana iguana*. (A) Trace of lateral bending of trunk. (B) Means and standard deviations of the activity of hypaxial muscles relative to trunk bending during walking. (C) Summary of foot support relative to trunk bending. The R or L in each activity box represent the phase of hindlimb support in which activity was predicted to occur, based on the hypothesis that the hypaxial muscles act to stabilize the trunk against horizontal, lateral and vertical components of the propulsive force.

described above. First, the pubic abdominis muscle was active during ipsilateral flexion and ipsilateral extension (Fig. 4). Second, results from the retrahentes costarum were ambiguous. In one specimen, this muscle exhibited activity during ipsilateral extension and contralateral flexion, much like that of the internal oblique. However, in another animal, three separate electrodes, which recorded unambiguous activity during ventilatory expiration, exhibited highly variable activity during walking.

Onset and offset times of muscle activity were independent of stride frequency over the range of frequencies analyzed (0.39–1.72 strides s^{-1}). For example, linear
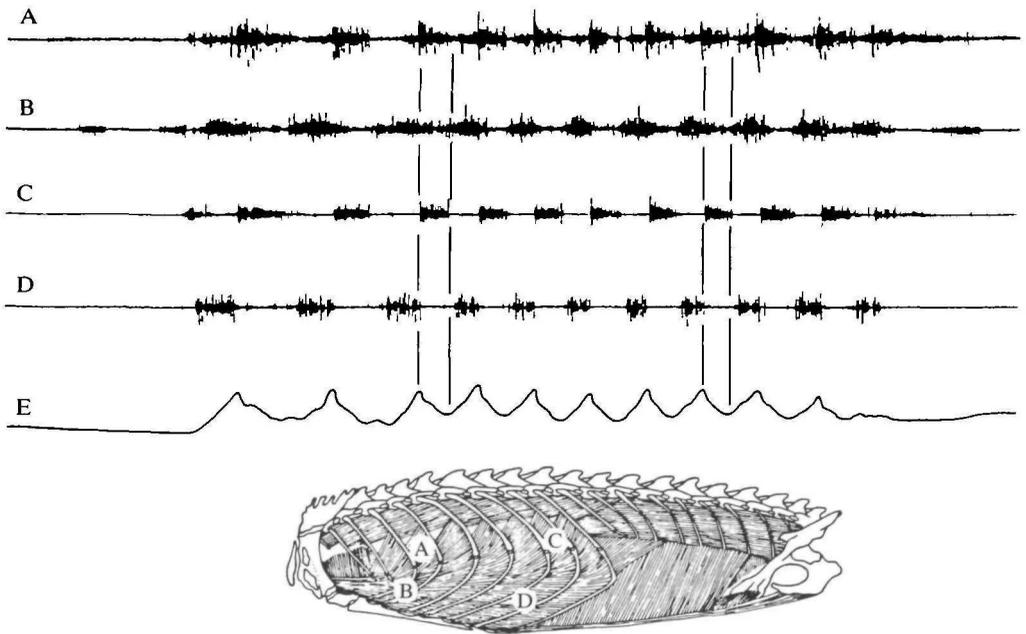
Fig. 5. Activity of the m. intercostales interni of *Iguana iguana* during walking. (A–D)
Recordings of activity from the left side of the body. Sites of electrodes are shown in
the diagram of the muscle. (E) Recording of trunk bending. A rise in the trace
indicates bending of the trunk to the left.

regression of onset time and offset time of the external oblique against stride
frequency yielded r^2 values of 0.025 and 0.108 ($N=30$), respectively.

Discussion

For reasons that are not clear, the role that the hypaxial muscles play in
locomotion has been almost completely ignored. Only limited recordings of
muscle activity have been made. Tokuriki (1973*a,b*, 1974) analyzed the activity of
several trunk muscles, including the external oblique and rectus abdominis, during
walking, trotting and galloping in dogs, but he provided little interpretation of his
results. The fact that the hypaxial muscles are most often associated with the
function of lung ventilation may explain why their locomotor role has received so
little attention. Alternatively, the lack of attention may be due to a human bias
resulting from our bipedal posture and striding gait, which reduces the role of the
trunk in locomotion. In any case, the results presented here represent the first
systematic survey of the activity patterns of the hypaxial muscles during loco-
motion in a tetrapod.

The results of this investigation indicate that the hypaxial muscles of green
iguanas do play a role in locomotion. Nine of the 10 muscles tested displayed
rhythmic electromyographic activity during even the slowest walking. This is in

marked contrast to activity of the hypaxial muscles during lung ventilation in these animals, in which only portions of four hypaxial muscles displayed activity (Carrier, 1989). Thus, the hypaxial muscles are locomotor muscles.

Although the results support the hypothesis that the hypaxial muscles contribute to lateral bending of the trunk, the pattern of activity is not consistent with this function alone. The most obvious means of accomplishing lateral bending would be for one or more of the hypaxial muscles with longitudinal components to their orientation to be active on one side of the body while all those with longitudinal components on the other side are silent. However, in actuality, there is simultaneous activity on the two sides of the body, but in different muscles on either side. This suggests that the hypaxial muscles do more during locomotion than simply bend the body from side to side.

Stabilization of the trunk during locomotion

During walking and running, the propulsive force produced by the limbs can be divided into three components: vertical, horizontal and lateral (Gray, 1968). These three components also act in the opposite direction on the trunk, at the joint between the limb and girdle. The horizontal component is responsible for the forward motion of the animal and induces a rotational torque on the girdles (Fig. 6A,B). The lateral component tends to bend the trunk at 90° to the desired direction of travel, and also exerts a rotational torque on the girdles (Fig. 6A). The vertical component, acting against gravity, induces long-axis torsion in the trunk (Fig. 6C). If the animal is to move forward in an efficient manner, the trunk must be stabilized against these torques in a manner that allows transmission of the supportive and horizontal components to the centre of gravity.

Stabilization of the girdles and vertebrae during locomotion could be accomplished solely by compressive elements (i.e. bone) or by tensile elements (i.e. ligament). However, compressive or passive tensile struts would work only if they fixed the trunk in a rigid or almost rigid state, as in terrestrial arthropods. Alternatively, because muscles can act as tensile elements of variable length, they could stabilize the trunk and provide flexibility of movement as well. To accomplish this, the hypaxial muscles with longitudinal and oblique fibre orientations would have to be active in a predictable pattern (Fig. 6).

The activity patterns of the hypaxial muscles of *Iguana iguana* are consistent with the hypothesis that they function to stabilize the trunk against the propulsive force. First, stabilization of the girdles against the horizontal and lateral components of the propulsive force requires that hypaxial muscles with fibres oriented longitudinally be active on the side of the trunk contralateral to hind support (Fig. 6A). Activity of the rectus abdominis, the deep portion of the external oblique and the ventral portion of the internal intercostal match this prediction. Second, stabilization of the trunk against the vertical forces inducing long-axis torsion requires that hypaxial muscles with fibres oriented obliquely in the anterio-dorsal direction be active on the side of the trunk contralateral to hind support (Fig. 6C). The superficial portion of the external oblique and the external

intercostal match this prediction. Finally, resistance to long-axis torsion also requires that hypaxial muscles with fibres oriented obliquely in the anterio-ventral direction be active on the side of the trunk that is ipsilateral to hind support (Fig. 6C). Activity of the internal oblique and lateral portion of the internal intercostal are consistent with this. Thus, seven of the nine muscles with longitudinal or oblique orientations match the predictions of the hypothesis. This suggests that obliquely oriented hypaxial muscles act to stabilize the trunk against long-axis torsion resulting from the vertical component of the propulsive force,
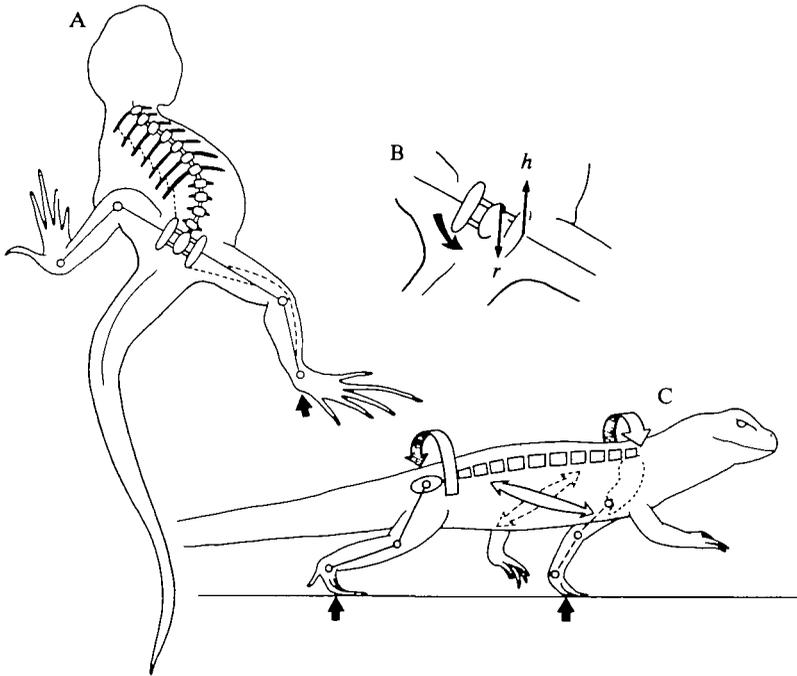
Fig. 6. Schematic representations of the moments imposed on the trunk during locomotion. (A) The lizard is exerting a force against the ground with the right hindleg. The inertial mass of the animal resists the propulsive force with a reaction force that acts rearwards through the centra of the vertebrae. (B) This reaction force (r) and the horizontal component of the propulsive force (h) at the hip joint produce a couple that tends to rotate the pelvis, in this case causing the pelvis to rotate counter clockwise. In addition, the lateral component of the propulsive force also exerts a counter clockwise rotational torque on the pelvis, due to the action of the muscles of the thigh (dashed lines in A) acting around the right hip joint. To stabilize the pelvis against these forces, muscles on the left side of the trunk with a longitudinal orientation (dashed lines in A) must be active. (C) The lizard is supported by diagonal limbs (filled arrows), which impose long-axis torsion (curved arrows) on the axial musculo-skeletal system. To stabilize the trunk against long-axis torsion, hypaxial muscles with oblique orientations are necessary. The solid white arrow indicates the orientation of muscles that must be active on the side of the body ipsilateral to hind support. The dashed white arrow indicates the orientation of muscles that must be active on the side of the body contralateral to hind support.

and that longitudinally directed muscles resist forces tending to rotate the girdles in the horizontal plane.

The activity pattern of the internal intercostal muscle is particularly intriguing in this regard. The internal intercostal consists of lateral and ventral portions, with different fibre orientations. These two regions are active during opposite phases of the locomotor cycle. The anterio-ventrally directed lateral portion is active ipsilateral to hind support, as would be expected if it were actively resisting long-axis torsion. In contrast, the longitudinally directed ventral portion is active contralateral to hind support, as would be expected if it were resisting horizontal rotation of the girdles and vertebrae.

The pattern of activity observed in the longitudinally directed muscles (i.e. *ra*, *oep* and *iiv*) is, however, also consistent with the function of lateral bending of the trunk. Lateral bending is generally thought to increase stride length and thereby contribute to the propulsive effort. However, in lizards, the amplitude of lateral bending is inversely related to running speed (Daan and Belterman, 1968). This is the opposite of what would be expected if the purpose of lateral bending was to increase stride length. Alternatively, lateral bending of the trunk may be largely a passive consequence of the trunk muscles acting to stabilize the trunk against the horizontal and lateral components of the propulsive force. In any case, it is entirely possible that the hypaxial muscles accomplish both lateral bending and stabilization.

Three muscles cannot be incorporated into the hypothesis. First, the transversalis has a predominantly transverse orientation and, therefore, is largely unable to resist lateral or torsional moments on the trunk. Consequently, its activity during ipsilateral hindlimb support must be associated with some other aspect of locomotion. Second, the pubic abdominis was predicted to be active ipsilateral to hind support to resist torsional moments. However, its location and orientation are such that it could also resist the horizontal and lateral moments exerted on the pelvis. Its activity during maximum ipsilateral flexion may be a compromise between these two demands. Third, the retrahentes costarum was also predicted to be active ipsilateral to hind support to resist torsional moments. In one specimen it did exhibit this pattern. However, in another animal the activity was variable during walking. The retrahentes costarum is an expiratory muscle that is associated with the nine thoracic ribs and may have a primarily ventilatory function.

Seven of the nine muscles tested (excluding the transversalis) matched the predictions (Fig. 4). Thus, the mechanics of locomotion seem to provide a functional explanation of the basic organization of the hypaxial muscles. There are two reasons to suspect that the pattern of hypaxial activity observed here in iguanas will be characteristic of tetrapods as a group. First, most groups of tetrapods display the same basic organization of the hypaxial muscles. Groups that differ in a significant manner are unlikely to generate large lateral and torsional moments on their girdles, because they are either limbless and girdleless (snakes and caecilians) or specialized in symmetrical loading of the trunk (frogs). Second,

the mechanics of limbed locomotion suggests that the proposed model of hypaxial action will apply to all species that move with a striding quadrupedal or bipedal gait. However, at present, similar data have not been collected from other species, so it is not yet possible to say how inclusive the pattern is.

Configuration of the intercostal muscles

The organization of the intercostal muscles has long been argued to be a consequence of the mechanics of lung ventilation. The most widely held view is based on simple mechanics and can be traced back to the early eighteenth century (Hamberger, 1727, De Troyer et al. 1985). The anterio-dorsal orientation of the external intercostal gives its posterior insertions longer moment arms around the centre of rotation of the ribs than those of the anterior insertions. Hence, when the muscle contracts, the moments tending to move the ribs anteriorly will be greater than those tending to rotate the ribs posteriorly. In contrast, the anterio-ventral orientation of the internal intercostal results in larger moments tending to rotate the ribs posteriorly than those tending to rotate them anteriorly. Thus, the external intercostals should increase thoracic volume and be inspiratory in function, whereas the internal intercostals should effect expiration. Experimental support of the hypothesis has come out of early electromyographic studies on mammals (Bronk and Ferguson, 1935; Taylor, 1960).

However, there is increasing evidence that the two intercostal muscles do not display this antagonistic pattern. In mammals (Gesell, 1936) and birds (Kadono et al. 1963; Fedde et al. 1964), anterior portions of the external and internal intercostals are active during inspiration, whereas posterior portions of the two muscles are active during expiration. Green iguanas are similar, in that anterior segments of both intercostals are active during inspiration (Carrier, 1989). However, neither muscle is involved in expiration. Thus, instead of acting as antagonists, the two intercostal muscles work as synergists to ventilate the lungs. In contrast to the traditional view, the different fibre orientations of the two intercostal muscles seem to have little significance for ventilatory function. Furthermore, experiments in which portions of the intercostal muscles of dogs were selectively stimulated suggest that the ventilatory action of the intercostal muscles is determined not by fibre orientation, but by the relative resistance of the ribs to anterior versus posterior displacement (De Troyer et al. 1985). These experiments suggest that a single intercostal muscle would be sufficient for the purposes of breathing. Consequently, lung ventilation alone does not provide a functional explanation for the configuration of the intercostal muscles.

This investigation has shown that the intercostal muscles play a role in locomotion. Yet the configuration of these two muscles remains enigmatic. On the one hand, their activity during locomotion matches perfectly the hypothesis that they stabilize the trunk against the vertical, horizontal and lateral components of the propulsive force. On the other hand, their fibre orientation and activity during locomotion make them seemingly redundant with the two oblique muscles. Furthermore, the absence of intercostals in salamanders demonstrates that they

are not essential to terrestrial quadrupedal locomotion. In the light of the available evidence, it seems reasonable to suggest that the configuration of the intercostal muscles represents a compromise between the demands of locomotion and ventilation. Locomotor function requires two layers with radially opposed, oblique orientations and ventilatory function requires costal muscles that are separate and independent of the oblique muscles.

In summary, the hypaxial muscles of green iguanas do participate in locomotion. Those muscles with oblique orientations appear to stabilize the trunk against the vertical component of the propulsive force, which induces long-axis torsion in the axial skeleton. Those muscles that have longitudinal orientations appear to function in stabilizing the trunk against the horizontal and lateral components of the propulsive force. However, the observations of this investigation cannot rule out the possibility that longitudinally oriented muscles also produce lateral bending of the trunk. Although, this study reports on data gathered from only a single species of lizard, other groups of tetrapods can be expected to exhibit the same basic pattern.

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