Exp Brain Res (1998) 119:324–332

RESEARCH ARTICLE

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The cat vertebral column: stance configuration and range of motion

Received: 2 January 1997 / Accepted: 23 September 1997

Abstract This study examined the configuration of the vertebral column of the cat during independent stance and in various flexed positions. The range of motion in the sagittal plane is similar across most thoracic and lumbar joints, with the exception of a lesser range at the transition region from thoracic-type to lumbar-type vertebrae. The upper thoracic column exhibits most of its range in dorsiflexion and the lower thoracic and lumbar in ventroflexion. Lateral flexion is limited to less than 5° at all segments. The range in torsion is almost 180° and occurs primarily in the midthoracic region, T4-T11. Contrary to the depiction in most atlases, the standing cat exhibits several curvatures, including a mild dorsiflexion in the lower lumbar segments, a marked ventroflexion in the lower thoracic and upper lumbar segments, and a profound dorsiflexion in the upper thoracic (above T9) and cervical segments. The curvatures are not significantly changed by altering stance distance but are affected by head posture. During stance, the top of the scapula lies well above the spines of the thoracic vertebrae, and the glenohumeral joint is just below the bodies of vertebrae T3-T5. Using a simple static model of the vertebral column in the sagittal plane, it was estimated that the bending moment due to gravity is bimodal with a dorsiflexion moment in the lower thoracic and lumbar region and a ventroflexion moment in the upper thoracic and cervical region. Given the bending moments and the position of the scapula during stance, it is proposed that two groups of scapular muscles provide the major antigravity support for the head and anterior trunk. Levator scapulae and serratus ventralis form the lateral group, inserting on the lateral processes of cervical vertebrae and on the ribs. The major and minor rhomboids form the medial group, inserting on the spinous tips of vertebrae from C4 to T4. It is also proposed that the hypaxial muscles, psoas major, minor, and quadratus lumborum could support the lumbar trunk during stance.

Key words Vertebral column · Antigravity support · Scapula · Cat

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Introduction

Most studies of postural control in both bipeds and quadrupeds have focused on the limbs, whereas the trunk has been treated as a single segment in kinematic models. A more complete understanding of postural control requires examination of the trunk and axial skeleton. Because the majority of body mass lies in the trunk segments, it is important to understand how the trunk is supported against gravity during stance and how it is stabilized against external perturbations. The preceding report (Macpherson and Fung 1998) described the activity of thoracic and lumbar epaxial extensors during postural responses to translations of the support surface. Muscles in the thoracic and in the lumbar regions exhibited opposite responses to the same perturbation, and a small transition zone was found between the 10th and 12th thoracic levels. The activity in lumbar epaxial muscles appeared to be related to stabilizing the pelvis, but the role of the thoracic and the transitional muscles during postural responses was less clear. This study was undertaken to determine the range of motion of the vertebral column and its postural orientation during stance. The aim was to gain a better understanding of both the antigravity support of the trunk and of the activation pattern of dorsal back muscles.

Several authors have speculated on trunk mechanics of quadrupedal mammals (e.g., Badoux 1968; Gray 1944; Thompson 1992), but these studies have suffered from a lack of concrete data regarding kinematics and electromyographic (EMG) data. Kinematic studies of the axial skeleton are technically difficult and require either invasive techniques (Dufosse et al. 1982) or imaging approaches. Most atlases typically depict the axial skeleton with a simple concave, downward curve between the first thoracic and the last lumbar vertebrae and a horizontally oriented cervical column (e.g., Crouch 1969; Gilbert 1975; Reighard and Jennings 1901). Recent X-ray imaging studies have revealed that the cervical column of many quadrupeds is held not in the horizontal position, but in the vertical position during resting postures (Graf et al. 1995a, b; Keshner 1994; Selbie et al. 1993; Vidal et al. 1986). No one to our knowledge has yet analyzed the geometry of the entire thoracolumbar complex.

Materials and methods

These studies were performed with the approval of the institutional IACUC and conform to the NIH guidelines regarding the principles of laboratory animal care. Seven cats (six males and one female) varying in weight from 3.8 to 4.7 kg were used for radiographic analysis of the vertebral column while in various stance postures or maximally flexed positions (i.e., joint angles characterizing maximal bending of the axial system as a whole). Five of these animals were subjects in the previous study (Macpherson and Fung 1998). For the X-rays in maximal positions, the animals were anesthetized with a mixture (0.15 ml/kg) of acepromazine (1 mg/ml) and ketamine (100 mg/ml) and held in position during the radiographic exposure. For the sagittal plane views, X-rays were accepted for further analysis only if the vertebrae were well focused and showed no out-of-plane orientation. Fluoroscopic examination was used for the lateral bending position to ensure that there was no torsion of the vertebral column. Again, X-rays were inspected to ensure that the vertebrae were oriented in the desired plane with the vertebral spines well-centered in the dorsal view.

Four cats were used for the maximally flexed positions. Each animal was placed either on its side or prone on the table and was held in the position of maximal dorsiflexion, ventroflexion, left and right lateral flexion, and left and right torsion (around the rostrocaudal axis). Because of the size of the animals, it was not always possible to include the full vertebral column in one X-ray, in which case emphasis was placed on capturing the thoraco-lumbo-sacral region. Fluoroscopy was used to position the cats in lateral flexion because of the tendency for the vertebral column to rotate around the long axis during lateral bending motion. Examining the column first with fluoroscopy allowed us to be sure that all vertebrae were aligned vertically and the image of each spine was centered with respect to the vertebral body. Because the field of view of the fluoroscopic device was small, it was necessary to take two X-rays, in which the images overlapped.

Radiograms were taken of four cats during quiet stance, of which one was also in the group used for maximally flexed positions. The animals stood freely on four small wooden blocks that were similar in size to the force plates on which they were trained to stand (see Macpherson et al. 1987 for details). The X-ray film was mounted vertically, immediately adjacent and parallel to the long axis of the animal. Radiograms were taken during stance at three different distances between fore- and hindlimbs, the preferred distance of the animal and plus and minus 40% of that distance. The preferred distances ranged from 25 to 30 cm across cats. Stance was not constrained except for paw separation, but food and attention were used to encourage the cat to orient its head in a forward facing position. Again, X-rays were accepted for further analysis only if the vertebrae were well focused and showed no out-of-plane orientation.

Radiograms were analyzed using a similar technique to that described by Graf et al. (1995a), but, rather than measuring by hand with a light box, the X-rays were digitized using a scanner (HP ScanJet IIcx) and the images were imported into a drawing program (Canvas, Deneba). Using the program, fine lines were drawn on each vertebral image to indicate the long axis and its orientation. The lines were aligned with the lower border of the spinal canal (see Fig. 1), unlike the study by Graf and colleagues (1995a), who used the lower border of each vertebra for the orientation axis. We found that the vertebral canal provided a more regular measure across the different vertebral morphologies of the thoracolumbar column. The sacrum provided one exception, since the canal shows a curved profile. The axis of the sacrum was determined by a line joining the lower border of the canal at anterior and posterior aspects. The angles between adjacent vertebrae were determined using the angle-measuring function in Canvas. Means and standard deviations of angles were calculated across cats and the means were used to determine maximal excursions at each joint as well as changes from the standing posture. Stance data from one cat (So) was excluded from the means, because this animal was found to have only six lumbar vertebrae.

The method of measuring intervertebral angles is subject to error owing to possible misalignment of vertebrae outside the plane of the X-ray, varying quality of the image mainly due to changes in density, especially in the region of the scapulae, and errors in estimating the axis of the vertebral canal. However, the method as described by Graf and colleagues (1995a) produced quite similar results to another study by Selbie and colleagues (1993), which used a more complex rigid-body analysis for estimating the centers of rotation of the vertebrae. Another, possibly more accurate method, would have been to implant small radio-opaque markers on each vertebra and use these as landmarks for calculating angles (Keshner 1994). Given the number of vertebrae in the thoracolumbar column, this method was deemed impractical. Finally, even if the absolute measures of intervertebral angle have some error associated with them, the more important relative measures of range of motion and the comparison of stance angles to the maximum ranges are still valid because of the consistency in the methodology.

Results

Figure 1 shows a typical X-ray image for a cat in the standing position. The inset is an enlargement of the segments from T12 to L2, showing the lines drawn to indicate the axes of the vertebrae. It was generally more difficult to determine structural details in the upper thoracic and cervical regions, because the image of the scapulae tended to obscure that of the vertebrae. Often, the cervical segments were not included on the radiogram because of the animal's size, particularly for the maximally dorsiflexed position. In general, it was not difficult to determine the axis of the spinal canal for each vertebra. In those cases where the image was more obscure, the canal orientation of a vertebra was interpolated by drawing a line that intersected the lines for each of the two adjacent vertebrae in the region of the intervertebral disc spaces.

Passively flexed positions

All four cats showed a similar profile of intervertebral angles in the dorsiflexed position. The largest intervertebral angles were in the lower cervical and upper thoracic region, C6 to T7 on average (Fig. 2A). In only one cat was it possible to visualize and measure upper cervical angles, therefore little can be said about this region of the column in dorsiflexion. Even in the dorsiflexed position, some angles near the thoracolumbar junction (T11-L1) maintained a degree of ventroflexion in each cat.

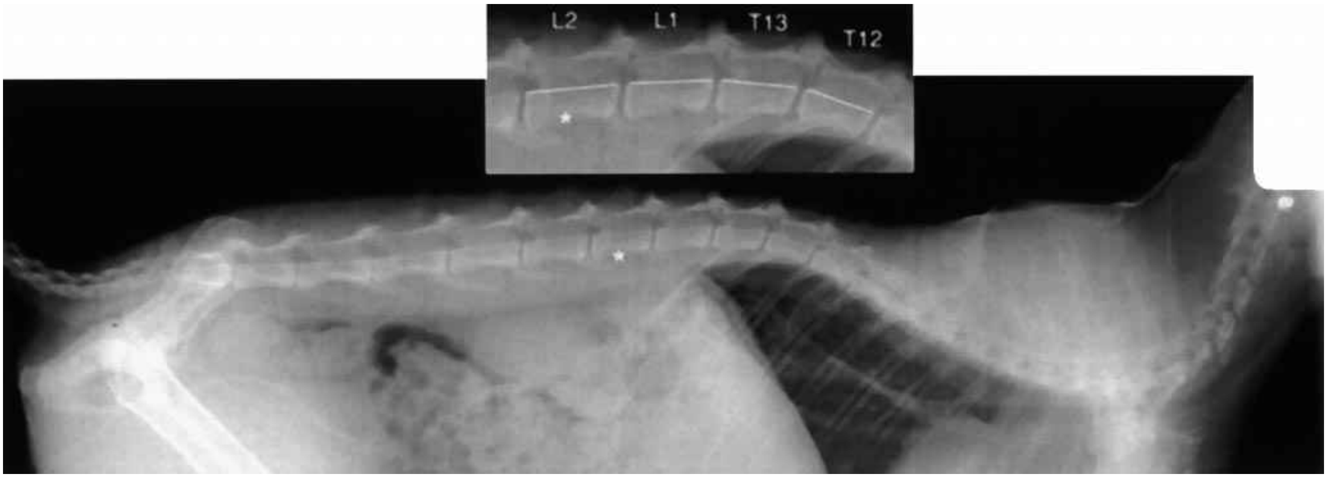


Fig. 1 X-ray of a cat (Rg) standing at its preferred fore-hindlimb distance (28 cm). The *inset* is a higher magnification of the lower thoracic and upper lumbar segments, to illustrate how angles were measured. The *asterisk* marks the L2 vertebra on each image. The *white lines* were drawn onto a scanned image of the X-ray to indicate the orientation of each vertebra using the landmark of the ventral border of the spinal canal. The angles between adjacent vertebrae were then determined using the angle-measuring tool in Canvas

Thus, in dorsiflexion, the vertebral column maintains at least three curvatures, a dorsiflexion in the lumbar area, a ventroflexion near the thoracolumbar junction, and a prominent dorsiflexion in the upper thoracic and lower cervical regions.

In the ventroflexed position, the largest intervertebral angles were in the lower thoracic and upper lumbar region, T11-L4, and in the cervical region, C2-C5 (Fig. 2B). Note that, for this position, cervical angles were measured in all four cats up to the C2-3 junction. Joint angles were small (less than 5°) and variable in the upper thoracic region, but angles between all vertebrae were in the direction of ventroflexion on average. The degree of ventroflexion decreased gradually in the lower lumbar region to almost zero between L6 and L7, but showed a significant increase at the joint between L7 and the sacrum (6.5° on average). Carlson (1978) also found considerable range of motion at the L7-sacral joint.

Figure 2C shows the sagittal plane range of motion of the intervertebral joints, obtained by subtracting the angles at dorsiflexion from those at ventroflexion. The degree of flexibility was fairly uniform, with a few exceptions. The upper thoracic vertebrae (C7-T3) showed the largest range. Note that the cervical segments are excluded from the mean because of the limited data set for dorsiflexion. There was a restriction of mobility in the lower thoracic region (T9-10 and T10-11 joints on average) and even more so at the L6-7 joint.

Left and right lateral flexion measures were averaged across cats. Lateral flexion was surprisingly limited at all the joints and evenly distributed along the vertebral column (Fig. 2D). The large variability in these measures

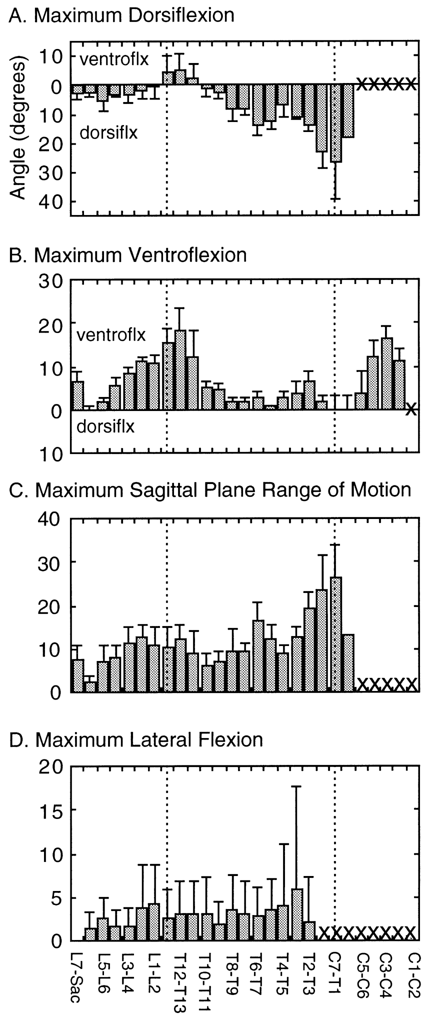


Fig. 2A-D Means and standard deviations of intervertebral angles. **A** Dorsiflexion (four cats) **B** Ventroflexion (four cats). **C** Sagittal plane range of motion. Within each cat, dorsiflexion and ventroflexion angles were combined to compute a total range of motion at each joint. These values were averaged across the four cats and plotted as mean and SD. **D** Lateral flexion (three cats). *Vertical dotted lines* indicate the boundaries between the thoracic and lumbar vertebrae and the cervical and thoracic vertebrae. *X*s indicate the joints that were not possible to measure in at least two cats because of limitations in contrast or in X-ray size

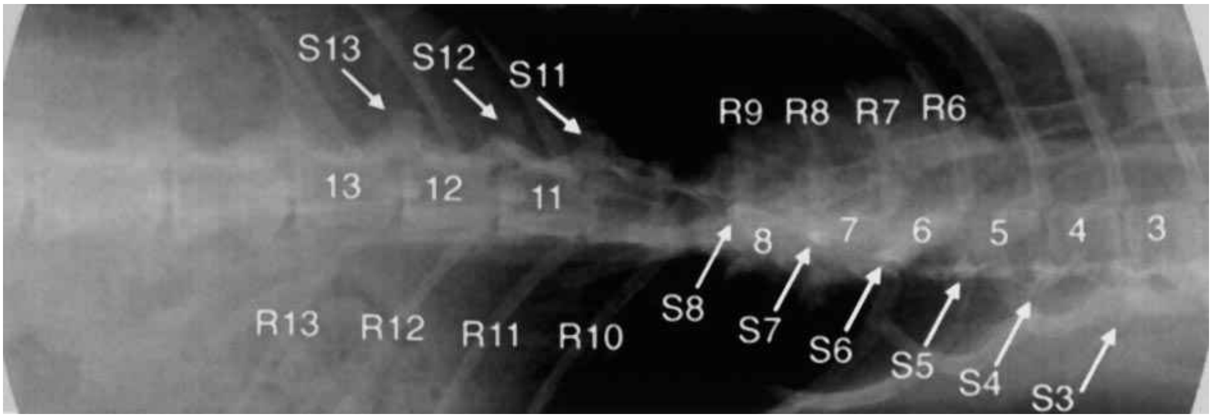


Fig. 3 X-ray showing torsion. Caudal is to the *left* and rostral to the *right*. The hindlegs point down relative to the figure and the forequarters are rotated to the animal's left such that the forelegs point up relative to the figure. Thoracic vertebral bodies are indicated by *number*. Vertebral spines are indicated by the *arrows* and labeled *Sx*, where *x* represents the level. Ribs are indicated by an *R* and the appropriate *number*. Note that the last two thoracic spines (S12 and 13) are oriented upward, indicating that torsion does not begin until about T11. Almost all torsion is complete by about T4, where the vertebral spine is oriented downward

may be due to variation in the sagittal plane curvature of the vertebral column of each animal in the prone position. Mechanical interference of the lateral processes of two adjacent vertebrae may change depending on their sagittal plane angle. Most of the cat's apparent flexibility in lateral motion actually results from torsion, or rotation around the long axis of the column. Note that fluoroscopic monitoring was used prior to the X-ray to prevent any torsion in the laterally flexed position.

Torsion

Three cats were X-rayed in maximal torsion to left and right. Each showed a remarkable flexibility with a total torsion along the vertebral column of almost 180°. Most of the torsion was seen within a small range of the lower thoracic vertebrae from about T4 to T11 (Fig. 3). Neither the lumbar nor the upper thoracic vertebrae exhibited any significant range of motion in torsion. The cervical vertebrae were not studied in torsion.

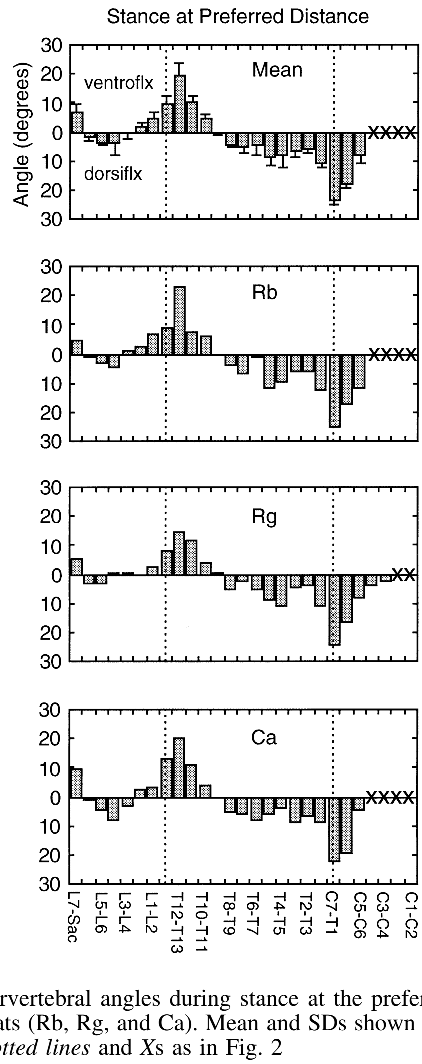


Fig. 4 Intervertebral angles during stance at the preferred distance for three cats (Rb, Rg, and Ca). Mean and SDs shown in *top panel*. *Vertical dotted lines* and *X*s as in Fig. 2

Active stance

Figure 1 shows an X-ray of cat Rg standing at the preferred distance of 28 cm. Unsupported, quiet stance was characterized by four curvatures from the sacral to the lower cervical regions (Fig. 4). First, the L7-sacral angle showed a significant ventroflexion of 7° on average. The adjacent lower lumbar angles showed a mild dorsiflexion up to about L4-5. The next curvature was a marked ventroflexion in the lower thoracic-upper lumbar region, with a maximum angle of 17° at the T12-13 joint. Finally, there was a second and prolonged dorsiflexion throughout the upper thoracic and lower cervical regions, beginning at the T8-9 joint and extending at least up to the C6-7 joint, which was as far as could be reliably measured. The angles remained relatively constant at about 8° up to the cervicothoracic junction, where they increased to a maximum and then decreased. The points of inflection

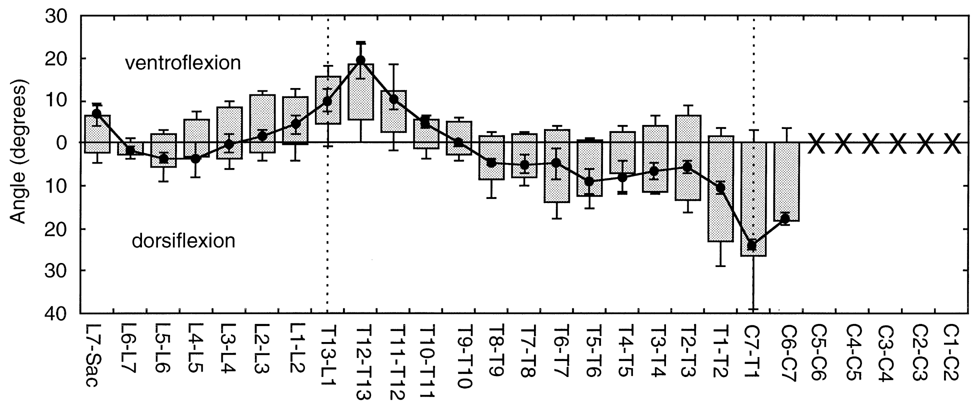


Fig. 5 Mean stance angles relative to range of motion. *Boxes with SD bars* indicate the range of motion in the sagittal plane at each intervertebral joint. *Filled circles* indicate the mean angles measured for stance at the preferred distance. *Vertical dotted lines* and *X*s as in Fig. 2

of the curvatures were approximately at L6-7, L3-4, and T9-10.

A surprising finding was the position of the scapula relative to the vertebral column during stance, as illustrated in the X-ray of Fig. 1. The shoulder joint was located immediately below the bodies of T2 and T3 in all cats. The scapular spine was oriented backward at an angle of about 20° from vertical. The vertebral border of the scapula was considerably above the level of the thoracic spines such that an average of 23% of the scapular length extended above the spine tips (range 11–38%). The top of the scapula measured at the scapular spine lay directly above the T4 vertebral body on average (ranging from T3-4 joint to T4-5 joint).

Figure 5 shows a plot of the mean intervertebral angles during quiet stance (filled circles) superimposed on a bar chart indicating the maximal angular range in dorsi- and ventroflexion to illustrate the stance configuration relative to the joint angular limits. Only the means were used for this comparison, because the data came from mostly different cats (only one animal was used for both maximal positions and quiet stance). From this comparison it appears that, during stance, the lower lumbar joints (L4-5 to L6-7) are nearly maximally dorsiflexed. Furthermore, the joints from T10 to T13 inclusive appear maximally ventroflexed. In general, the other joints are held midrange, but closer to their dorsiflexion than to their ventroflexion limits. The angles between adjacent vertebrae were not significantly affected by altering stance distance (Fig. 6). The curvatures remained similar, as illustrated by the bottom bar chart showing negligible difference between the angles at the short stance distance and those at the long distance.

A fortuitous pair of X-rays in one animal suggest that head position may have a significant effect on spinal curvatures (Fig. 7, cat So). For the top plot, the head was stretched forward toward the food dish, whereas for the bottom plot the head was retracted. The latter position is one often adopted when a cat is startled by a looming visual stimulus. When the head was extended forward, all the curvatures of the back even down to the lumbar level were seen to decrease. These data illustrate the range of possible angles during stance.

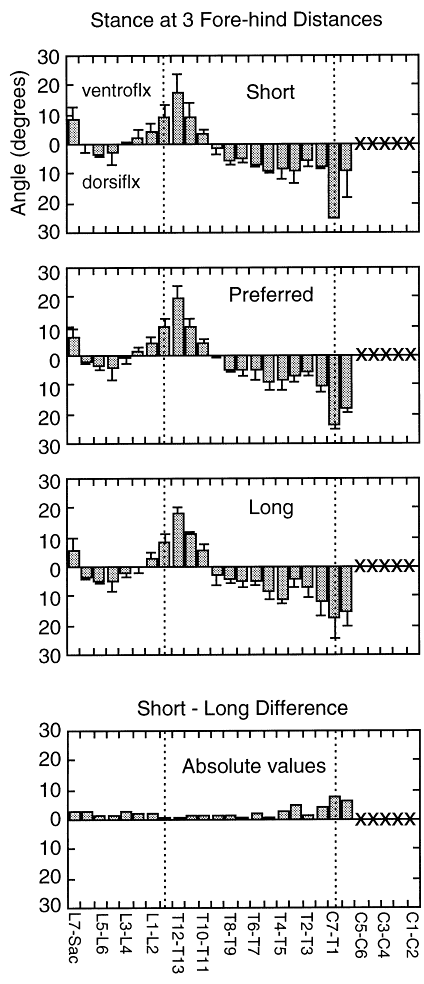


Fig. 6 Mean intervertebral angles at three stance distances (n=3). *Vertical dotted lines* and *X*s as in Fig. 2. The *bottom panel* shows the absolute value of the difference in each mean intervertebral angle between the long and short stance distances

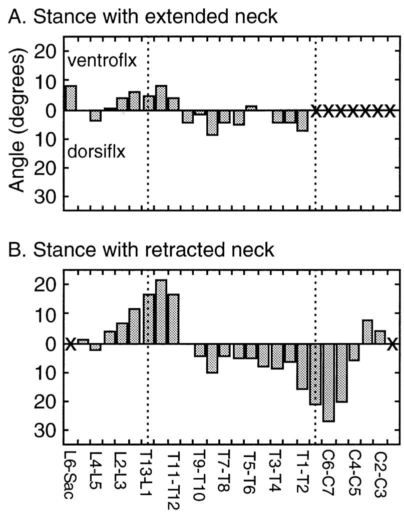


Fig. 7 Intervertebral angles in cat So at two different head positions, noted during the shooting of the X-ray. Cervical vertebrae were visible only on the X-ray of the retracted head position and not the extended. Note that this animal had only six lumbar vertebrae. *Vertical dotted lines* and *X*s as in Fig. 2

Model

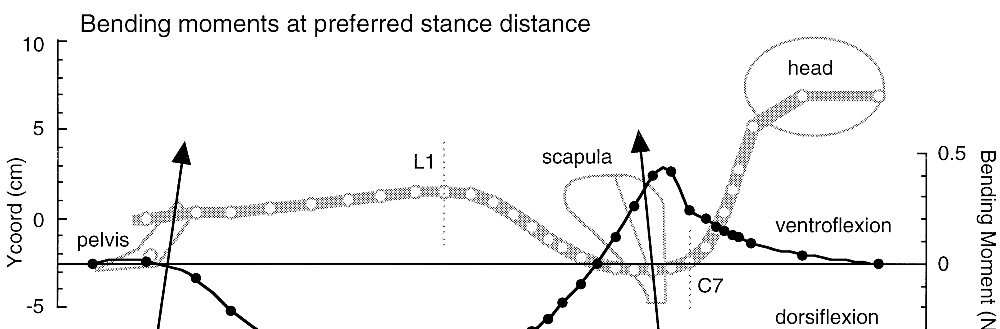
Using the typical curvatures observed during quiet stance, a simple static model of the vertebral column was generated in order to explore the mechanical constraints upon the axial skeleton and the requirements for stability during stance. Measurements of axial segment dimensions were made from a disarticulated skeleton, and spatial coordinates in the sagittal plane were calculated based on the intersegmental angles measured for quiet stance. Figure 8 shows the resulting schematic plot of the vertebrae, pelvis, scapula, and skull.

The bending moment due to gravity under static conditions was computed at each intervertebral joint based on the following assumptions. The mass of the animal was set at 4 kg, which is within the range of our past and present feline subjects. The mass distribution among the various segments and the position of the center of mass of each segment (lumbar trunk, thoracic trunk, neck, and head) were based on published data (Hoy and Zernicke 1985). The vertebral column was assumed to be a rigid structure. The following assumptions were based on averaged data published previously (Fung and Macpherson 1995): the ratio of vertical reaction forces under fore- and hindlimbs was fixed at 56:44; the ground reaction force under the forelimbs was assumed to pass through the glenohumeral joint; the orientation angle of the forelimb ground reaction force was 84.9° (see Fig. 8).

An interesting feature of cat forelimb anatomy is that the scapulae do not articulate with the axial skeleton. Instead, the trunk is supported by muscles that originate on the medial surface of the scapula near the dorsal border and fan out to insert on the trunk in a sling-like arrangement. The *net* suspensory force vector between scapula and trunk was assumed to be colinear with the forelimb ground reaction force vector and therefore intersected the vertebral column near the T2-3 joint.

The hindlimb ground reaction force was calculated to be 96.5°, given that the fore- and hindlimb horizontal forces are equal and opposite. This angle is well within the range of experimentally observed values. Finally, given the requirement for zero net vertical and horizontal forces and zero net moments, the point of application of the hindlimb ground reaction force on the vertebral column was computed. The position of this calculated force, about 1 cm in front of the hip joint (see arrow in Fig. 8) is quite consistent with observed values (Fung and Macpherson 1995).

Fig. 8 Model showing bending moments computed for each intervertebral joint. Sagittal plane coordinates of vertebral bodies and joints are indicated by *thick lines* and *circles*, respectively. *x*-axis represents anteroposterior coordinates and *y*-axis on the *left*, vertical coordinates; *y*-axis on the *right* indicates scaling for bending moments in newton-meters (*N.m*). Note that ventroflexion moments are upward and dorsiflexion, downward. *Vertical dotted lines* mark the cervicothoracic and the thoracolumbar joints. *Arrows* indicate ground reaction forces (*grf*)



The bending moment along the vertebral column was calculated using the method of sections (Parker and Ambrose 1992) and is illustrated in Fig. 8 (filled circles). The lumbar and lower thoracic regions exhibit a dorsiflexion bending moment with a maximum value near the L1-2 joint. In contrast, the upper thoracic and cervical column exhibits a ventroflexion bending moment with a maximum at the point of application of the forelimb reaction force. The point of zero moment is near the T5-6 joint.

Discussion

In quadrupedal mammals, the trunk is horizontally oriented and consists of a series of segments between the fore- and hindlimbs, the length of which depends on the species. The axial skeleton may be considered as a segmented beam with the legs as pillar supports and two overhanging regions, the head-neck segments and the tail. In the cat, there are typically 7 cervical, 13 thoracic, and 7 lumbar vertebrae. The vertebrae and their articulations are of two general forms (Crouch 1969). The upper thoracic and lower cervical vertebrae are short in length with long spines and form articulations that lie primarily in the frontal plane. The lower thoracic (T12 and T13) and lumbar vertebrae are long and have short, stout spines. Articulations are complex, with a mortice-and-tenon arrangement on either side, lying primarily in the sagittal plane. In the cat, the transition between the two vertebral types occurs across two segments, T10 and T11, the diaphragmatic and anticlinal vertebra, respectively. These latter two vertebrae have very short processes.

The range of motion in the sagittal plane is relatively uniform along the vertebral column, with some exceptions (Fig. 2C). Our measured range of motion was reasonably consistent with that shown by previous studies for the upper thoracic (above T3) and lower cervical joints (Graf et al. 1995a; Selbie et al. 1993).

The upper thoracic and cervical segments appear to be optimally arranged for dorsiflexion motion, whereas the lumbar and lower thoracic segments are predisposed for ventroflexion. Such specialization can be related to the typical behaviors of the cat. Dorsiflexion in the upper segments is necessary for achieving a wide range of head postures, particularly the vertical orientation of the cervical column. Ventroflexion of the lower segments allows for seated postures and facilitates locomotion, especially for in-phase gaits such as galloping (English 1980; Hildebrand 1959). The upper thoracic column is limited in ventroflexion by the ribs and thorax, whereas the lumbar area is limited in dorsiflexion by the vertebral articulations. The flexibility of the vertebral column in bending and especially in torsion allows the animal to achieve the contorted postures observed in behaviors such as grooming.

During natural stance, the vertebral column showed surprisingly complex curvatures, consisting of a dorsiflexion in upper thoracic and lower lumbar regions and a prominent ventroflexion from approximately T10 to L2. Previously, the trunk was assumed to conform to a simple arch shape with the convexity pointing upward (e.g., Crouch 1969; Gilbert 1975; Gray 1944; Thompson 1992). Similarly, it was long assumed that the neck was held in a near-horizontal orientation. Recent radiographic studies of the head and neck segments in awake animals have shown instead that the cervical column is maintained in a near-vertical alignment (Vidal et al. 1986). It is likely that the pronounced dorsiflexion of the thoracic region is necessary to achieve a vertical cervical column.

Another consequence of the complex curvatures is that lateral bending will be mechanically coupled with torsion during lateral motion of the trunk, particularly in the T4 to T11 region where torsional range of motion is pronounced. This suggests that translations of the standing cat outside of the sagittal plane will produce more complex forces on the vertebral column than just the lateral bending moments that were originally hypothesized (Macpherson 1994).

Another surprising observation was that a significant portion of the scapula lies above the spinous tips of the vertebrae. Previous publications typically show the top border of the scapula to be level with or even below the vertebral spines (e.g., Crouch 1969; Gans and Storr 1962; Gilbert 1975; Gray 1944; Thompson 1992). One older atlas by Jayne (1898) does, however, show a more accurate representation of the scapula and vertebral column.The relative position of the scapula to the upper thoracic column as well as the extreme thoracic dorsiflexion is confirmed in a recent radiographic study of the forelimb during locomotion (Boczek Funcke et al. 1996). This finding has important implications for the role of some scapular muscles.

The estimation of bending moments, although generated by a simple model, nevertheless is instructive in thinking about how the trunk is supported during stance. Many of the assumptions of the model are based on actual experimental data from our previous studies (Fung and Macpherson 1995). The computation of the position of the hindlimb ground reaction force vector was based on these assumptions and on the requirements of statics. The fact that the position of this vector was very similar to that observed in the experimental data provides for some confidence in the results of the model. The form of the bending moment curve is typical of a horizontal beam supported on two pillars and having one overhanging end (or cantilever). In the cat, the overhang consists of the head, neck, and rostral thoracic vertebrae (T1 to approximately T4). The mass of the tail is relatively small and does not contribute a significant moment, particularly when the tail is held in the typical pendular position. The vertical support pillars are the fore- and hindlimbs.

The lumbar dorsiflexion moment computed from the model is consistent with the observation that the lumbar epaxial extensors, multifidis, longissimus dorsi, and ilio-

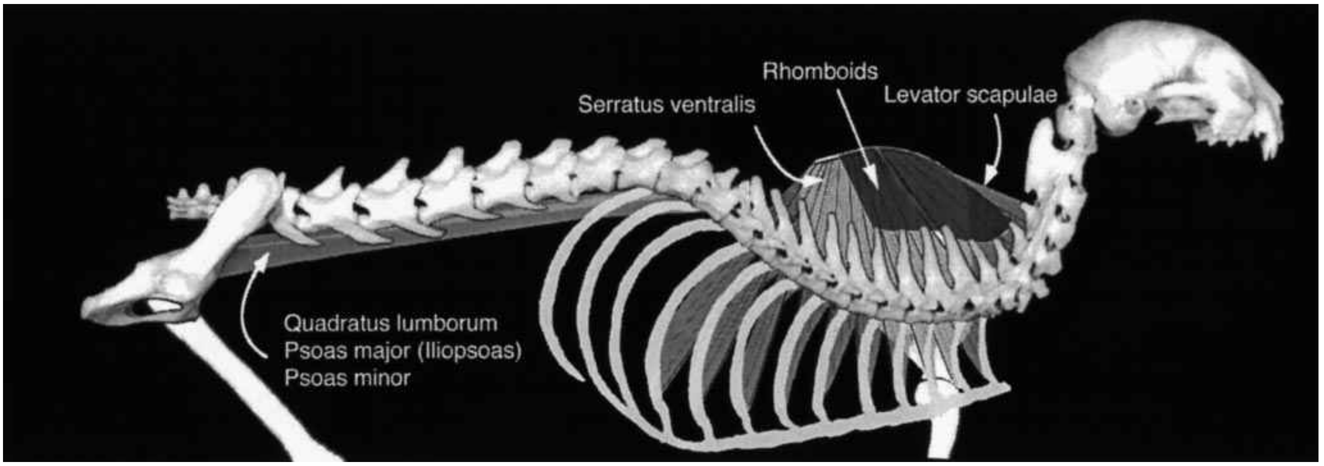


Fig. 9 Schematic representation of the sagittal plane geometry of the skeleton of the standing cat, based on X-ray measures, showing the muscles that are proposed to contribute to the antigravity support of the animal. The hypaxial muscles psoas major and minor and quadratus lumborum resist the dorsiflexion moment at the lumbar spine. Two groups of scapular muscles suspend the cervical and thoracic column from the scapula by their medial (rhomboids) and lateral (levator scapulae and serratus ventralis) attachments

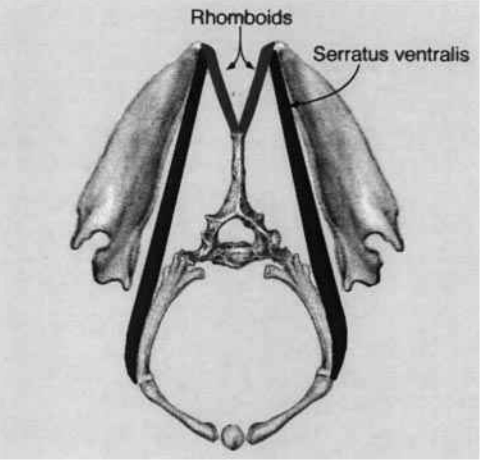


Fig. 10 Schematic representation of the frontal plane attachments of the two groups of scapula suspensory muscles. Note the three-point configuration of the muscular attachments to the trunk

costalis show little or no tonic EMG activity during stance (Macpherson and Fung 1998). Instead, the tendency of the lower thoracic and lumbar column to collapse in dorsiflexion could be resisted by tonic activity in the antagonist hypaxial muscles (Fig. 9). The psoas minor originates from the ventral surface of the vertebral bodies from T12 to L3 or L4 and inserts on the ilium of the pelvis just anterior to the hip joint. The quadratus lumborum lies more laterally, attaching to the ventral surface of the transverse processes of the vertebrae from T12 to L7 as well as the ilium. The psoas major, or iliopsoas, originates from the cranial tendons of psoas minor, the ventral surface of vertebrae L4 to L7 and the ventral border of the ilium and inserts on the lesser trochanter of the femur (Crouch 1969). All these muscles could produce a ventroflexion moment that would help support the lower trunk against gravity. The rectus abdominis, which runs from the pubic tubercle to the sternum, has a long moment arm for ventroflexing the lumbar trunk. However, this muscle is very thin and sheet-like in the cat and does not exhibit much tonic activity during stance (J. M. Macpherson unpublished observations).

The support of the upper thoracic and cervical column against gravity appears to require a very different mechanism from that described above for the lumbar axial skeleton. Both the computed ventroflexion moment and the anatomical arrangement of the scapulae with the trunk suggest a support analogous to that of a suspension bridge. We propose that the main antigravity support for the head, neck, and upper trunk is provided by two groups of muscles whose attachments join the scapula and the axial skeleton. Both groups of muscles originate on the vertebral border of the scapula (Figs. 9, 10). The first group, consisting of levator scapulae and serratus ventralis, fans out to insert laterally on axial segments from C3 to T9 or T10. Levator inserts on the transverse processes of the cervical vertebrae whereas serratus inserts on the ribs. The second group, consisting of the major and minor rhomboids, inserts medially on the tips of the spinous processes from C4 to T4. Because of the dorsal position of the origins of all these muscles relative to their insertions on the trunk, they will act to suspend the trunk from the scapulae much like the wires on a suspension bridge. From a frontal view, these muscles form a three-point suspension of the trunk (two lateral and one medial; see Fig. 10), which could act to stabilize it, particularly against rolling (torsion) movements that would be induced when one forelimb is lifted from the ground.

The suspensory action of serratus ventralis has been recognized by many authors (reviewed by English 1978), but the idea that levator and the rhomboids may also contribute to this function has not been previously recognized. This is probably due to the fact that previous authors have assumed that the thoracic spines are above or level with the vertebral border of the scapula, hence the typical description that these muscles pull the scapulae together (rhomboids).

We suggest that tonic activity in the two groups of scapular muscles during stance not only provides the main support for the cervicothoracic column but also shapes the curvature of this column. Because of the strong dorsiflexion curvature, a large part of the force due to gravity would be taken up in compression along the long axis of the vertebral bodies. During resting postures in the cat, the cervical joints are near the dorsiflexion limit up to C4-5 and then become more ventroflexed, particularly at the C2-3 joint (Graf et al. 1995a). It is noteworthy that this transition to ventroflexion is just above the most rostral insertion of the levator scapulae and the rhomboid minor. The proposal of serratus ventralis as the main antigravity support of the caudal thoracic trunk is consistent with our observations that the epaxial extensors of the upper thoracic region show little tonic activity during quiet stance (Macpherson and Fung 1998). There is evidence that serratus ventralis is tonically active during stance in the horse (Hall et al. 1991) and during the stance phase of locomotion in the cat (English 1978) and monkey (Schmitt et al. 1994). The rhomboids are also active during the stance phase of locomotion (English 1978). Levator scapulae shows high tonic activity during stance (J.M. Macpherson unpublished observations).

If these two groups of scapular muscles do provide the major antigravity support of the cervical and thoracic trunk, then these muscles would also be expected to play a major role in the adjustment of head position. Furthermore, head position in the sagittal plane would have an important mechanical impact on the curvatures of the vertebral column, as suggested in Fig. 8. Using levator scapulae and rhomboid minor to support the cervical column would minimize the need for tonic activity in the dorsal neck muscles. Indeed, upright resting postures are maintained by tonic activity in only a few dorsal neck muscles (Richmond et al. 1992). Rather than providing significant antigravity support, these latter muscles may instead act to fine-tune the relative positions of the cervical segments and their degree of extension.

The lack of significant effect of changing stance distance on the curvatures of the vertebral column confirms the previous kinematic analysis of postural orientation in the cat (Fung and Macpherson 1995). That study showed that different stance distances are accommodated by changing the inclination of the limb axes and not by altering trunk variables such as length and orientation.

Acknowledgements The authors gratefully acknowledge the skilled and patient technical support of Crista Barberini, Stephanie Jensen, and Dr. Charles Russell. We thank Barry Uchida of Oregon Health Sciences University for the use of the X-ray facility and for his invaluable assistance in obtaining the radiograms. We would also like to thank the following for their insights and encouragement during many helpful conversations: Dr. Jiping He, Dr. Ken Statler Dr. Kit Runge, and Dr. Ian Stokes. This work was supported by NIDCD (RO1-DC01356) and by a joint funding effort from NIDCD and NASA (P60-DC02072).

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