

MAMMALIAN SPINAL BIOMECHANICS

II. INTERVERTEBRAL LESION EXPERIMENTS AND MECHANISMS OF BENDING RESISTANCE

BY JULIANNA M. GÁL*

Department of Pure and Applied Biology, University of Leeds, Leeds, LS2 9JT, UK

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Summary

Three-point cyclic bending was applied to intervertebral joint complexes (three vertebrae with two intervertebral discs) of monkey (*Macaca fascicularis*), wallaby (*Wallabia rufogrisea fruticosa*), tiger (*Panthera tigris*), jaguar (*Panthera onca*) and seal (*Halichoerus grypus*). Force–displacement loops were recorded for intact specimens in both extension and flexion. Reductions in peak forces at given displacements were measured, following lesions of ventral ligaments, supraspinous ligaments, interspinous ligaments and muscles, ligamenta flava and the articular capsules. Subsequently, the vertebral arches were removed from the specimens to test the bending resistance of the intervertebral discs alone. The results of these lesion experiments, coupled with details of intervertebral joint anatomy, suggest that extension resistance is ultimately due to articular joint impaction for all species tested. The prominent ligamenta flava of the monkey and wallaby contrast with the robust discs of jaguar and tiger and illustrate two distinct mechanisms for resisting flexion in mammalian intervertebral joints. The conspicuous absence of soft structural elements in seal intervertebral joints contributes to their low bending resistance. The implications of these findings for mammalian locomotion, behaviour and scaling are discussed.

Introduction

Mammalian intervertebral joint construction is generally conserved across the Orders. The primary bony features, the vertebral centra, support the vertebral arches, which collectively house the spinal cord. The spinous, transverse, cranial and caudal articular processes, extensions of the arches and the centra, furnish attachment sites for the epaxial and abdominal muscular and ligamentous tissues. The intervertebral discs constitute the major articular sites; the synovial joints between adjacent articular processes provide important secondary articulations. Articular joint capsules and ligamenta flava complete the set of structures that bind the intervertebral joints, endowing them with both static and

*Present address: Human Performance Laboratory, Faculty of Physical Education, University of Calgary, 2500 University Drive NW, Calgary, Alberta, Canada T2N 1N4.

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dynamic mechanical properties. Differences between mammals are manifest largely by the degree to which such structures are enhanced or diminished.

Relatively few studies have involved successive lesioning of intervertebral structures to identify passive mechanisms of joint resistance. Tencer *et al.* (1982) performed extensive mechanical tests with cadaveric human intervertebral joints. They found that the intervertebral discs played the most vital role in limiting lateral and anterior shear, axial compression and flexion. The facets played a major role in resisting posterior shear and axial torque. Dumas *et al.* (1987) conducted tensile tests with human cadaveric intervertebral joints. Intervertebral discs were sectioned, leaving only the ligamentous attachments intact. The latter were sequentially resected and the tensile tests repeated. The most restrictive ligament was ligamentum flavum, followed by the articular, interspinous and supraspinous ligaments. Non-human lesion studies are even rarer. Smeathers (1981) conducted Euler buckling tests with rabbit and goat lumbar spines. Lesion experiments showed that flexion was resisted primarily by ligamenta flava in the rabbit and the intervertebral discs in the goat intervertebral joints.

Gál (1993) investigated the static and dynamic bending behaviour of the intervertebral joints of a variety of mammals. Results showed that scaling theory alone could not explain the mobility patterns observed. Statistical comparisons of mathematical parameters describing joint compliances suggested that flexion resistance was controlled by different structures in different species. Mathematical modelling and statistics are indispensable tools for predicting and detecting significant differences between joints, but they fall short of identifying the structures responsible for the observed bending properties. Therefore, a protocol of successive lesion experiments was carried out with intervertebral joint complexes, following the previous dynamic bending and strain energy tests. Extension and flexion bending cycles, within bending plateau ranges, were followed by serial cuts through the interspinous muscles and ligaments and the deeper articular capsules and ligamenta flava. Reductions in peak forces for given actuator displacements were indicative of reductions in joint resistance. The removal of the vertebral arches and associated structures allowed inferences to be made about the resistance capabilities of the intervertebral discs alone. The results of the lesion experiments and intervertebral joint dissections of this study are combined with the intact bending properties described in the previous paper to provide a more complete discussion of the functional morphology of the mammalian vertebral column.

Materials and methods

Lumbar–lumbar and lumbosacral intervertebral joint complexes, containing three successive vertebrae and two intervertebral discs, were isolated and mounted for three-point cyclic bending tests as described by Gál (1993, see Materials and methods, the dynamic bending experiments section for specimen numbers and source details). Force–displacement loops were recorded from intact joint complexes of monkey (*Macaca fascicularis*), wallaby (*Wallabia rufogrisea fruticosa*), jaguar (*Panthera onca*), tiger (*Panthera tigris*) and seal (*Halichoerus grypus*) (Burton, 1972; Burton and Burton, 1979; Burn, 1980). Successive lesions of intervertebral structures were performed with

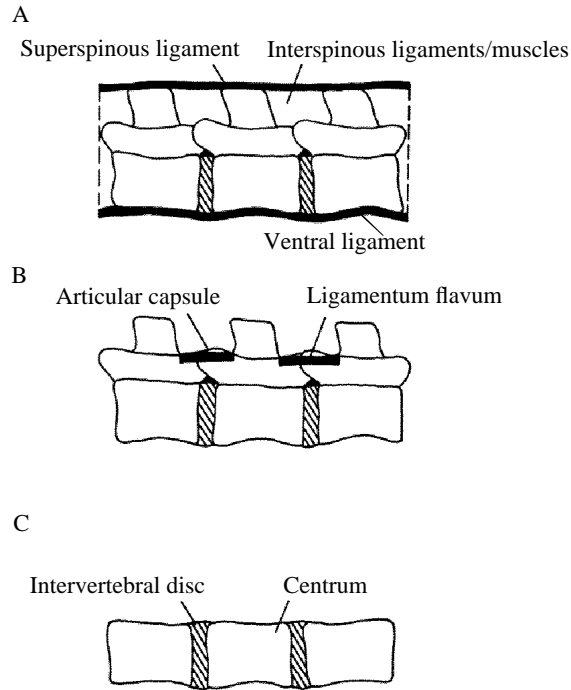


Fig. 1. The structures that were sequentially cut in the lesion experiments are illustrated. Symmetrical cuts were made across each joint and the bending cycles were repeated. See text for further explanation. A, B and C show different degrees of dissection.

scalpel and *post mortem* (PM) knife and bending tests were repeated. Reductions in peak forces for given actuator displacements were measured. The detailed protocol follows.

Ventral ligament

The ventral (or anterior) ligament is a ligament that connects the ventral surfaces of adjacent vertebral centra and discs. This continuous strip extends the entire length of the vertebral column. Because the axes of rotation of intervertebral joints presumably run through the middle of the discs and centra, the ventral ligament tends to resist joint extension (see Fig. 1A for a schematic diagram). Following the recording of a force–displacement loop for each intact specimen in extension, the actuator was lowered to expose the ventral surface of the centra (recall that, for these three-point bending tests, extension and flexion meant that the ventral surfaces of the centra and the spinous processes, respectively, rested on the two outer blocks). A scalpel or PM knife was used to sever this ligament midway along the ventral length of each centrum and disc. The actuator was returned to its original level and the extension test was repeated. Since the moment arms were unchanged, reductions in peak forces reflected reductions in resistive moments offered by the joints.

Superspinous ligament and interspinous ligaments and muscles

The superspinous ligament fuses with the spinous processes of adjacent vertebrae (see

Fig. 1A for a schematic diagram). Often it is closely bound to the aponeurosis of the longissimus dorsi muscle and the lumbodorsal fascia, making separation very difficult. Where separation was not possible (particularly in the jaguar and tiger), all three structures were included under the single heading of superspinous ligament. This structure tended to resist joint flexion. Following intact flexion tests (intact except for the severed ventral ligament from the previous extension tests), the actuator was lowered to allow cutting of the superspinous ligament between each joint. The actuator was returned to its initial setting and the bending cycle was repeated. The actuator was lowered several more times to allow cuts of varying depths through the interspinous muscular and connective tissues, effectively deepening the initial superspinous cut. Each cut was followed by the replacement of the actuator to its original level and a repeat of the bending cycle. Changes in peak flexion forces reflected changes in the resistive moments of the joints.

Articular joint capsules and ligamenta flava

Interspinous muscular and connective tissue was carefully dissected from between both joints of each specimen to expose the articular facet joints. These are synovial articulations between pairs of cranial and caudal articular processes of adjacent vertebrae. They can vary in structure from fairly simple areas of overlap to elaborate cradle-like constructions. Ligamentum flavum is a ligament that connects the dorsal aspect of adjacent vertebral arches (see Fig. 1B for a schematic diagram of both the articular joints and ligamentum flavum). It usually contains elastin, a rubber-like protein (Wainwright *et al.* 1976). Once the interspinous structures are dissected away, ligamentum flavum is usually visible through a gap between successive vertebrae. Sometimes, however, it is hidden by the overlapping bony plates on the floor of adjacent vertebral arches. Exposure of this ligament was sufficient in all test species here to enable lesion. Following dissection, the specimen was remounted in the clamp and reattached to the Instron load cell. A new intact flexion cycle was recorded for each demuscle specimen, based upon the same actuator displacement as in the intact specimens. Successive lesioning through ligamenta flava and up, around and between the articular joints was followed in turn by repositioning of the actuator and repeating the bending cycle. Changes in peak flexion forces were compared to the new maxima of the demuscle specimens for given displacements.

Discs and centra

Following the lesion of the articular capsules and ligamenta flava, a hacksaw was used to cut each specimen longitudinally through the vertebral arches. Fig. 1C is a schematic representation of the remaining specimen: three centra and two intervertebral discs. These new specimens were remounted for cyclic bending tests by the same protocol used for the intact specimens (Gal, 1993). Tests were carried out in both extension and flexion and corresponding force-displacement loops were recorded. X-radiographs were taken of resting and bent specimens. Bending moments were calculated from the moment arms measured from the X-radiographs and the force loops (as described in Gál, 1993). To estimate the contributions of the intervertebral disc to the bending resistance of the intact

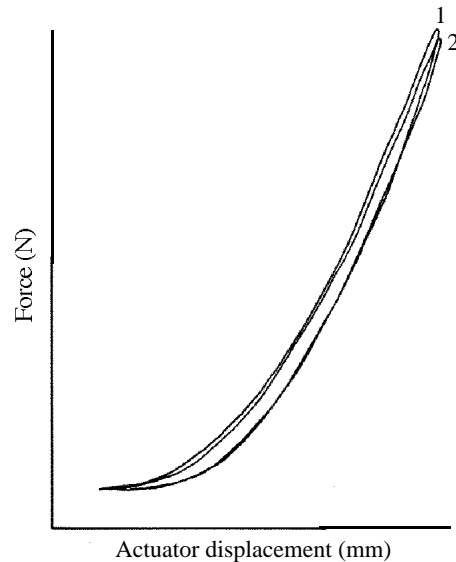


Fig. 2. The force–displacement loops for the intact and lesioned wallaby joint complex L2L3L4, subject to cyclic extension moments, are shown. Maximum changes in intervertebral angle were $+2.5^\circ$ for each joint. Maximum specific moments were 0.046 and 0.077 Nm kg^{-1} for L2L3 and L3L4 respectively. Loop 1 represents the force–displacement response of the intact joints. Loop 2 followed lesion of the ventral ligaments. See text for further explanation.

intervertebral joints, the observed changes in intervertebral angle for discs and centra were compared to the predicted changes in intervertebral angle for the corresponding intact joints. This was done by substituting the observed discs and centra bending moments into the appropriate bending equations for the intact joints (see Gál, 1993, Tables 2–5 inclusive) and calculating predicted changes in intervertebral angle.

Lumbar intervertebral joints from monkey, wallaby, tiger, jaguar and seal were examined by careful dissection and successive boiling and bleaching. This allowed scrutiny of the deeper intervertebral structures. Particular attention was given to the soft structural tissues.

Results

Figs 2–4 illustrate some examples of the responses of wallaby, seal and monkey and tiger joint complexes, respectively, to the lesion experiments described. A summary of the reductions in peak forces is shown in Table 1. Peak extension forces changed very little following lesion of the ventral ligament. The most dramatic reductions in peak flexion forces (for demuscle specimens) followed the lesion of ligamenta flava and the articular capsules of the monkey and wallaby (approximately 90 and 80% reduction respectively). Much smaller changes in peak flexion forces were observed for jaguar and tiger complexes (approximately 19 and 10–12% respectively).

Table 2 shows the results of the cyclic bending tests with discs and centra for monkey, jaguar and seal. Wallaby and tiger complexes were also tested but corresponding X-rays

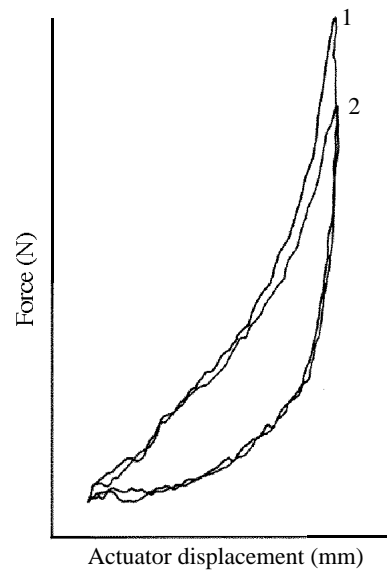


Fig. 3. The force–displacement loops for the intact and lesioned seal joint complex L1L2L3, subject to cyclic flexion moments, are shown. Maximum changes in intervertebral angle were -7.5 and -10° for L1L2 and L2L3 respectively. Maximum specific moments were -0.0020 and $-0.0033 \text{ Nm kg}^{-1}$ for L1L2 and L2L3 respectively. Loop 1 represents the force–displacement response of the intact joints. Loop 2 followed lesions of the interspinous ligament and interspinous muscles and ligaments. See text for further explanation.

were not taken. Predicted changes in intervertebral angles for intact monkey joints were much lower than those observed for monkey discs and centra subjected to the same bending moments. In contrast, predicted and observed changes in extension angle were similar in jaguar and seal. A similar, if not more pronounced, pattern was seen in flexion. Predicted changes in intervertebral angles were virtually the same as observed changes in jaguar and seal. Predicted changes for monkey were again much smaller than the observed changes.

Fig. 5 illustrates mid-lumbar intervertebral joint anatomy of monkey, wallaby, jaguar and seal (in sagittal and dorsal perspectives). These schematic representations emphasize the approximate positions and relative sizes of the intervertebral discs and ligamenta flava in the species.

Monkey

Monkey lumbar joints had rather small intervertebral discs that were thicker in the ventral half than in the dorsal half. Transverse processes were bent approximately half way along their length so that they terminated in a cranial direction in close association with the lateral aspect of each disc. Ligamentum flavum was a prominent yellowish ligament that appeared to extend dorsally from the vertebral arches to span the gap between adjacent spinous processes. It would seem, therefore, to have been an interspinous ligament as well. Articular joints were formed by the superposition of the

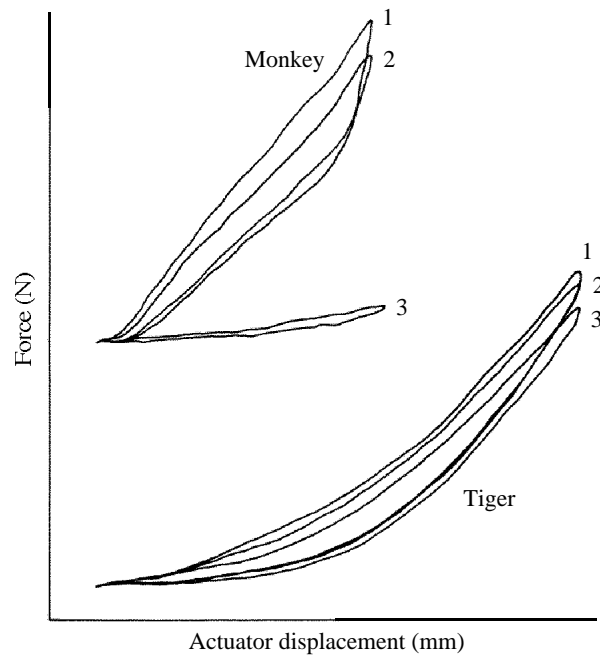


Fig. 4. The force-displacement responses of intact and lesioned monkey (L5L6S) and tiger (L3L4L5) joint complexes, subject to cyclic flexion moments, are shown. Maximum changes in intervertebral angle for the monkey joints were -4.5 and -6° (for L5L6 and L6S respectively) and maximum specific moments were -0.039 and $-0.036 \text{ Nm kg}^{-1}$ (for L5L6 and L6S respectively). For the tiger joints, maximum changes in intervertebral angle were -6.5 and -4° (for L3L4 and L4L5 respectively) and maximum specific moments were -0.051 and $-0.031 \text{ Nm kg}^{-1}$ (for L3L4 and L4L5 respectively). Loops 1 represent the force-displacement responses of the intact demuscle joints. Loops 2 follow lesion of the articular capsules. Loops 3 follow complete cuts through (inactivation of) ligamenta flava and the articular capsules. See text for further explanation.

Table 1. *Approximate percentage reductions in peak joint complex forces following lesions of intervertebral structures*

Animal	Cut ventral ligament (ext)	Cut superspinous ligaments, interspinous ligaments and muscles (flex)	Cut articular capsules and ligamenta flava (flex)
Monkey	—	5–18	90
Wallaby	0–8	0–12	80
Jaguar	0	14–22	19
Tiger	0	8–23	10–12
Seal	1	19	19

Reductions in peak forces at given displacements for intact and intact-demuscle joint complexes, and following lesion of intervertebral structures, are shown for each species tested. See text for further explanation.

Table 2. *Observed and predicted changes in intervertebral angle for discs and centra in extension and flexion*

		Moment mass (x)	$\Delta\theta_{iv}$ observed	Bending equation	$\Delta\theta_{iv}$ predicted (y)
Extension					
Monkey	L5L6 d/c	0.065	+27	$y=+6.4 (1-e^{-31.1x})$	+5.6
	L6S d/c	0.081	+27	$y=+9.6 (1-e^{-16x})$	+7.0
Jaguar	L3L4 d/c	0.14	+6.5	$y=+3.5 (1-e^{-58.4x})$	+3.5
	L4L5 d/c	0.16	+7	$y=+3.1 (1-e^{-63.2x})$	+3.1
Seal	L6L7 d/c	0.051	+6	$y=+6 (1-e^{-55.5x})$	+5.6
	L7S d/c	0.047	+11	$y=+8.4 (1-e^{-25x})$	+5.8
	L5L6 d/c	0.0031	+13	$y=+19.3 (1-e^{-154.2x})$	+7.4
	L6S d/c	0.0053	+7.5	$y=+17 (1-e^{-253.7x})$	+12.6
Flexion					
Monkey	L5L6 d/c	0.062	-19	$y=-10.3 (1-e^{-19.2x})$	-7.2
	L5L6 d/c	0.063	-18	$y=-10.3 (1-e^{-19.2x})$	-7.2
	L6S d/c	0.078	-22	$y=-23.1 (1-e^{-4.2x})$	-6.4
	L6S d/c	0.080	-19	$y=-23.1 (1-e^{-4.2x})$	-6.6
Jaguar	L3L4 d/c	0.18	-7	$y=-6.2 (1-e^{-94x})$	-6.2
	L4L5 d/c	0.18	-6.5	$y=-4.9 (1-e^{-50.8x})$	-4.9
	L6L7 d/c	0.095	-10	$y=-8.5 (1-e^{-89.5x})$	-8.5
	L7S d/c	0.088	-12.5	$y=-11.2 (1-e^{-46.6x})$	-11
Seal	L5L6 d/c	0.0045	-11.5	$y=-13.6 (1-e^{-282.7x})$	-9.8
	L6S d/c	0.0076	-11	$y=-10.2 (1-e^{-334.3x})$	-9.4

The results from the discs and centra bending experiments are summarized. The applied specific bending moments are shown, with the observed changes in intervertebral angle. $\Delta\theta_{iv}(\text{predicted})$ is the calculated change in intervertebral angle one would expect, if the specific moments applied to the discs and centra were applied to the intact joint complexes. These calculations are based on the negative exponential models of the particular joints and the direction of bending (from Gal, 1993). See text for further explanation.

caudal articular processes of the more cranial vertebra with the cranial articular processes of the caudal vertebra of the adjacent pair. Articular joint capsular material fused with ligamentum flavum such that they were very difficult to separate. Spinous processes sloped very slightly cranially and were quite short and blunt.

Wallaby

Like the monkey, the wallaby had relatively small, ventrally thickened intervertebral discs. Transverse processes sloped ventrally and cranially to overlap the area of the discs. Ligamentum flavum was a robust yellowish structure and was very closely associated with the articular joint capsules. Caudal articular processes of the more cranial vertebra of adjacent pairs formed cradle-like supports for the large cranial articular processes of the more caudal vertebra. Spinous processes were large tapering processes with slightly cranial orientations.

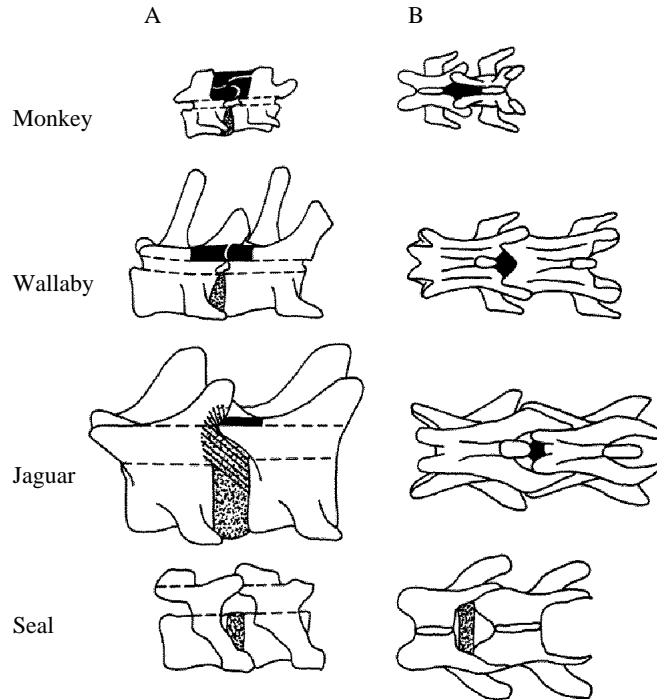


Fig. 5. Intervertebral joint anatomy of typical mid-lumbar joints of monkey, wallaby, jaguar and seal, are shown in sagittal (A) and dorsal (B) views. The intervertebral discs are highlighted by stippling. Ligamenta flava are indicated by the blackened areas. Ligamenta flava were most prominent in the monkey joints and virtually absent from the seal joints. Jaguar (and tiger) joints featured robust intervertebral discs, where outer annulus fibres appeared to extend around the articular joints (indicated here by the parallel lines extending from the stippled area). See text for further explanation.

Jaguar

Jaguar transverse processes were relatively short, with a slight ventral and cranial orientation. Unlike the monkey and wallaby, jaguar intervertebral discs were very prominent structures. Further, white (presumably collagen) fibres, appearing to originate from the dorsal half of the discs, fused with the vertebral centra around the site of the articular joints. The articular joints were also cradle-like in nature, with prominent cranial processes of the more caudal vertebra being supported by the smaller caudal processes of the more cranial vertebra of an adjacent pair. Ligamentum flavum had the yellowy appearance observed in the monkey and wallaby although, relative to the other intervertebral structures, it was much less substantial. Spinous processes were thick short structures, with a slight taper and cranial orientation. Similar features were observed for tiger mid-lumbar joints, which were larger in all respects.

Seal

Transverse processes of the seal again had a slightly ventral and cranial slope, terminating in a space overlapping the intervertebral discs. However, the seal joints

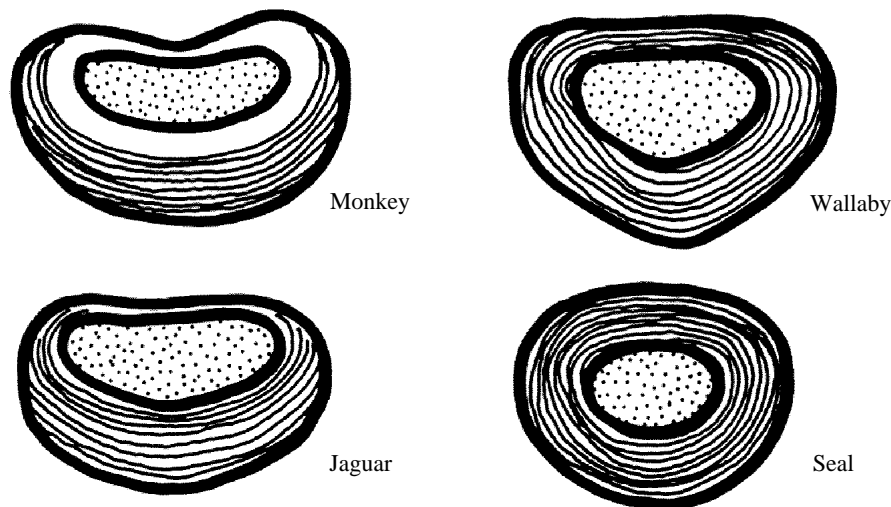


Fig. 6. The intervertebral discs of mid-lumbar intervertebral joints of monkey, wallaby, jaguar and seal are shown schematically in cranial cross-section. The stippled areas represent the nucleus pulposi. The outer areas represent the annulus fibrosi. See text for further explanation.

differed markedly from those of the other species examined; they were conspicuous in their almost total lack of soft structural tissue. Ligamentum flavum was reduced to a very fine strip of weak connective tissue, such that the intervertebral discs were clearly visible between the centra. Large spaces were evident between the vertebrae, exposing the vertebral canal. Intervertebral discs were reasonably thick structures that had a slightly concave profile, rather than the convex outline of the intervertebral discs of the other species studied. The articular joints had approximately vertical orientations, where caudal processes of the more cranial vertebra lay medial to the cranial processes of the more caudal vertebra of adjacent pairs. Spinous processes were very short, wide and blunt.

Fig. 6 shows schematic diagrams of cross sections through mid-lumbar intervertebral discs of monkey, wallaby, jaguar and seal. In normal healthy discs, two distinct components can be identified: the nucleus pulposus and the annulus fibrosus. The nucleus pulposus is the central gel-like component, composed primarily of water and a diffuse network of collagen fibres and proteoglycan molecules. The annulus fibrosus is made up of several lamellae containing strong, white, collagenous fibres. Collagen fibres are parallel within each lamella. Fibre orientation varies between lamellae, so that the macroscopic pattern of the annulus is a criss-cross weave (Panagiotacopoulos *et al.* 1987a,b,c; Shirazi-Adl, 1989a,b). These two components were distinctly visible in all four species and they looked superficially similar. However, the terrestrial species differed from the seal in that they all had asymmetrically placed nuclei. In the monkey and jaguar and to a slightly lesser extent the wallaby, the ventral half of the annulus was greatly thickened. The nucleus was dorsally displaced. The nucleus pulposus of the seal was more centrally located, with annulus thickness being dorsally, ventrally and laterally symmetrical. The annulus lamellae appeared to permeate through to the nucleus in all species except the monkey, where the annulus phase without the lamellae appeared

opaque-white but distinct from the gel. The lamellar fibres looked similarly white in all species.

Discussion

This study began with an investigation of intervertebral sagittal mobility in a series of mammals differing in size, locomotor mode and taxonomic lineage. Of the seven terrestrial species initially considered, only the monkey, wallaby and tiger were chosen for the dynamic bending tests and lesion experiments presented here. Intervertebral joints from these animals were lacking in measurable neutral zones and flexed more readily than extended. Mathematical modelling of the results of bending tests showed that wallaby and monkey joints had greater flexion capacities and were relatively stiffer than homologous tiger and jaguar joints (Gál, 1993). Here, successive lesion of intervertebral muscular and ligamentous tissue showed that passive resistance to flexion moments was due largely to tension in ligamenta flava and the associated articular capsules in monkey and wallaby intervertebral joints. In contrast, the intervertebral discs of tiger and jaguar joints were the most important structures in resisting passive flexion moments. Passive extension moments were resisted largely by articular joint impaction in monkey and wallaby joints. Intervertebral disc compression and articular joint contact both appeared to play roles in resisting passive extension moments in homologous tiger and jaguar joints.

Successive lesion of intervertebral structures to determine resistance hierarchy has been employed in relatively few studies. Tencer *et al.* (1982) performed static mechanical tests with human cadaveric lumbar intervertebral joints. Extension and flexion tests were included in their protocol. Changes in intervertebral angle and displacements of joint centres were recorded following lesions of the anterior (ventral) ligament, posterior (interspinous, supraspinous and intertransverse) ligaments and anterior discs fibres and facet removal. They found that lesion of the anterior ligament and 50% of the anterior disc fibres did not change any of the position parameters of the joint. They suggested that extension resistance resulted from bulk compression of the disc. Likewise, flexion resistance appeared to be largely the result of disc compression. Only with large displacements were the posterior ligaments and articular capsules shown to play a role.

Smeathers (1981) conducted lesion experiments with rabbit and goat lumbar vertebrae in order to correlate the results of buckling experiments with the intervertebral components. He found that, while flexion resistance in rabbit joints was due primarily to tension in ligamenta flava, resistance to flexion moments was due mainly to intervertebral disc compression and articular joint impaction in homologous goat joints. Articular joint contact was almost entirely responsible for limiting extension in the goat, whereas only in extreme extension did impaction act to limit extension in the rabbit joints.

It would appear, from the albeit limited number of documented cases, that similarities in the fundamental mechanisms of intervertebral flexion resistance exist between species and that these transcend differences in posture, locomotor mode and taxonomy. In rabbits, monkeys and wallabies, ligamentum flavum is the most important resistive element for intervertebral flexion. In humans, goats, tigers and jaguars, the most resistive

component for intervertebral flexion is the intervertebral disc. It is suggested that there may be a scale-dependent shift in the emphasis of particular intervertebral structures, based upon the material composition of those structures. In other words, there may be a shift from primarily elastin-containing to primarily collagen-containing structures with increasing animal size.

Elastin is a highly extensible rubber-like protein. Purified samples of ligamentum nuchae (80% elastin with a small amount of collagen and other materials) break at roughly twice their resting length. Its elastic modulus, about $6.0 \times 10^5 \text{ Nm}^{-2}$, is very similar to that of other protein rubbers (Wainwright *et al.* 1976; Gosline, 1980). Collagen is a very stiff material in tension. The Young's modulus of vertebrate tendons (dry mass about 70–80% collagen, Wainwright *et al.* 1976) is about $1.5 \times 10^9 \text{ Nm}^{-2}$ (Bennett *et al.* 1986). However, it has an ultimate strain of about 0.08–0.10 (Wainwright *et al.* 1976) and is therefore rather inextensible. So, elastin is relatively compliant with high extensibility, while collagen is relatively stiff with low extensibility. The great mobility of seal lumbar joints has been attributed, at least in part, to the lack of soft structural tissue. This is not a viable solution for joint mobility in terrestrial mammals because of gravitational considerations. Incorporating a highly extensible material like elastin would allow considerable changes in intervertebral angle, while maintaining joint integrity. However, since elastin is relatively compliant, the volume of material required to support the relatively greater bending stresses associated with increasing body mass could become prohibitive. Structural proteins are metabolically costly to synthesize and maintain and, therefore, it might be more economical in large animals to switch to a collagenous system for passive spinal resistance in order to keep the required volume of material to a minimum.

If intervertebral joint mobility is required, the problem then becomes one of building an extensible, yet stiff, collagenous structure. Tendon collagen fibres display a crimped or wavy pattern under light and electron microscopy. Tensile tests with mammalian tendons typically show low initial stiffnesses (toe regions), corresponding to regions where these crimps presumably straighten. Crimp straightening would allow limited low-resistance deformation before the fibres become stiffer. Additionally, if fibres are positioned obliquely to the direction of the applied stress, they will initially be loaded in shear. If loading continues, the fibres will become progressively reoriented until they are parallel and therefore loaded in tension. A structure composed of obliquely oriented collagen fibres could also permit a degree of relatively compliant deformation, before becoming stiff. The robust intervertebral discs of the jaguar and tiger could perhaps allow these processes to take place. Annulus lamellae are composed of helically wound collagen fibres embedded in a matrix through which shear could take place. The shearing process is associated with considerable hysteresis. The low resilience measurements for flexing jaguar and tiger joints, compared to homologous monkey and wallaby joints (approximately 35 and 65% respectively, see Gál 1993), are consistent with shearing phenomena. A shift or gradation from a predominantly elastin to a predominantly collagenous system may be the way to accommodate the mobility and structural integrity required by some large mammals, while minimizing energetic costs associated with the synthesis and maintenance of structural materials.

To test this idea, it would be useful to conduct similar dynamic bending and lesion experiments with intervertebral joint complexes from taxonomically related mammals of different sizes. The cat family would be a good group to study because gross morphology is conserved despite the wide range of sizes. The working hypothesis might be that flexion resistance would be determined by tension in ligamenta flava in the intervertebral joints of a domestic cat. This would contrast with the observed dependency upon the intervertebral discs in the tiger and jaguar intervertebral joints of this study. The inclusion of a cheetah in the investigation would make it even more interesting, given its superior sprinting capabilities. Another group that would prove useful to investigate would be the bovids. Halpert *et al.* (1987) studied lumbar vertebral morphology in a range of African bovids. They were concerned with dimensions of vertebral centra and processes and possible scaling relationships. Most of their vertebrae were museum specimens, so morphological comments were limited to those about the vertebral bone. Gross vertebral morphology of the smaller dik-dik was quite different from that of homologous eland vertebrae, particularly with respect to the relative size and orientation of the transverse processes. Smeathers (1981) distinguished between mammals with 'flexible' and 'stiff' backs, at least partly on the basis of differences in vertebral bony morphology. The results of these studies have demonstrated the importance of soft structural tissues (intervertebral ligaments and discs) in endowing particular stiffnesses to mammalian intervertebral joints. Given the differences in vertebral bone morphology, it would be of interest to examine the role of the soft structural tissues in bovid joints. Smeathers (1981) observed that many small mammals tended to have long arched 'flexible' lumbar columns, while many larger mammals tended to have short straight 'stiff' lumbar columns. He hypothesized that there was a trade-off between the energetic requirements of eliciting spinal movement and maintaining posture. Small mammals with flexible spines would be able to execute quick bending of the column, but would require constant axial muscle contraction to maintain a particular orientation. He surmised that the energy associated with maintaining posture as size increased would become prohibitive. Thus, large animals with passively stiff columns could maintain posture economically, at the relative expense of mobility.

However, maintaining any particular spinal orientation does not necessarily require axial muscle contraction if intervertebral ligaments behave like ligamentum nuchae, the robust supporting ligament of ungulates. Dimery *et al.* (1985) showed that ligamentum nuchae strain passively supported a substantial fraction of the total bending moment generated by the relatively heavy heads of sheep and camel. Thus, metabolic energy that would otherwise be consumed by contracting axial musculature would be conserved. Ligamenta flava were substantial intervertebral structures in the monkeys and wallabies studied here. Passive strain in these ligaments could be important in supporting postural bending moments, without compromising spinal mobility. In both species, the upper body is often left unsupported. The resting posture of a wallaby involves the tripod support of its hindlimbs and robust tail. Monkeys often sit upright during bouts of foraging and grooming. The role of passive intervertebral ligament strain has potential energetic implications for these two diverse species, the extent of which remains to be seen.

The marked sagittal compliance of seal lumbar–lumbar and lumbosacral joints first observed and quantified by Gál (1993) was shown to have an anatomical basis. The joints were virtually devoid of soft structural tissue, except the discs (see Fig. 5). Ligamenta flava were reduced to fine transparent strips, loosely associated with adjacent arches. The intervertebral discs could be seen at the floor of the vertebral canal. The articular capsules were weak structures; the articular joints were areas of simple overlap. The near-vertical orientation of the articular joints allowed considerable extension and flexion. Passive resistance would therefore be exerted primarily by the ultimate contact of the bony surfaces and tension in the disc (annulus) fibres. However, impaction of the articular joints appeared to occur only at very high, unlikely physiological angles. From a closer inspection of the X-radiographs, adjacent centra did not appear to make contact with each other. When a beam is bent, the concave and convex surfaces are subject to compressive and tensile forces respectively. If this analogy is extended to bending the intervertebral joints, then bony surfaces verge on impaction while annulus fibre tension is increasing. Therefore, it is difficult to separate these two effects. Seal intervertebral discs differed dramatically from those of terrestrial animals, not only with respect to the placement of the nuclei, but also in gross compressive properties. Adjacent joints could be grasped and squeezed together longitudinally with ease, by several millimetres. Therefore, it is unlikely that the intervertebral discs of the seal could exert substantial passive bending resistance, except perhaps at or near the extremes of joint movement.

Many anecdotal reports describe the grace and expertise of swimming pinnipeds. There are three families in the order Pinnipedia: Phocidae, Otariidae and Odobenidae, the true seals, eared-seals and walruses respectively. The harbour or common seal (*Phoca vitulina*) is a typical true seal, having sleek hair and no external ear-flaps. They swim almost exclusively with their hindflippers, using their foreflippers for steering. They stretch their hindflippers backwards and put the soles of their feet together in the vertical plane to form a type of vertical tail-fin. The hindflippers and hind end (to a certain extent) are then oscillated laterally in the horizontal plane. When the foreflippers are not being recruited for steering, they are held at the side of the body in depressions, thereby conserving their stream-lined body profile. Eared-seals, like the Cape Fur Seal, have thick fur and scroll-like external earflaps. They use their enlarged foreflippers as hydrofoils, effectively ‘flying’ through the water. With increasing speed, there may be the occasional vertical oscillation of the hind end and hindflippers. More often, however, the hindflippers are used for steering. So that while the eared-seals employ vertical oscillatory movements, true seals employ primarily horizontal oscillations to swim (Slijper, 1946; Burton, 1972; Burton and Burton, 1979; Burn, 1980; Feldkamp, 1987; Fish *et al.* 1988).

Equally anecdotal accounts of pinniped terrestrial locomotion are abundant. However, it is generally recognized that the eared-seals are far more agile on land than are the true seals. In eared-seals, body weight is supported clear off the ground on the outwardly turned foreflippers and the hindflippers, flexed forward under the body. Opposite foreflippers and hindflippers are moved alternately with only the heels making ground contact. Digits are held up as the foot is placed on the ground. As the speed of progression increases, first the hindflippers, then the foreflippers, become synchronous to give the

impression of a kind of gallop. The neck acts as an important counterbalance to maintain the balance of the body over the foreflippers. True seals are very awkward on land by comparison. They are unable to raise themselves on their foreflippers and equally unable to flex their hindflippers under their body. Instead, they progress by crawling or 'humping', flexing their bodies and taking their weight alternately on chest and pelvis (Slijper, 1946; Burton, 1972; Burton and Burton, 1979; Burn, 1980).

Hebrank (1982) investigated lateral bending and tensile properties of the backbones of Norfolk spot (*Leiostomus xanthurus*), a subcarangiform swimmer, and skipjack tuna (*Katsuwonus pelamis*), a thunniform swimmer. Bending properties reflected the mode of propulsion, with lateral mobility distributed throughout the length of the column in the spot and isolated in the caudal peduncle in the tuna. Movement in planes other than those resulting in net thrust generation were prevented by vertebral morphology. Oscillating streamlined bodies suffer greater friction drag than similar static streamlined bodies. Lighthill (1969, 1971) suggested that this phenomenon was due to thinning of the boundary layer. Even those animals that do employ body oscillations to propel themselves use some other strategy to reduce unwanted body oscillations or 'wagging'. Increasing depth of mid-section, either by adding large dorsal and/or ventral fins, or simply by deepening body profile, increases resistance to the turning moments generated by the oscillating caudal region. Fish *et al.* (1988) investigated the kinematics of swimming harp and ringed seals and estimated thrust production. They calculated drag coefficients and found them to be greater than those predicted for rigid streamlined bodies of similar size and shape. They commented that the propulsive lateral body and tail oscillations enhanced body drag by the mechanism previously described. They did not comment on the presence or absence of sagittal oscillations. To maintain sagittal rigidity during swimming, a seal would probably have to contract antagonistic axial muscles. This would tend to increase the energetic cost of swimming, relative to what it would be if sagittal rigidity were passively maintained. For these reasons, greatly enhanced sagittal mobility is probably not the greatest asset for an animal that swims by lateral oscillations of the hindflippers.

However, an effectively limbless semi-aquatic mammal, destined to return to the land or pack-ice to breed and moult, might just find that sagittal mobility is a necessity. It is suggested that the enhanced sagittal mobility observed in the common and grey seals (specimens from Gál, 1993, the static and dynamic bending tests respectively) and probably all true seals, is an adaptation of these semi-aquatic mammals to locomotion on land. With the exception of the somewhat laterally displaced iliocostalis muscle, most of the axial musculature of the seal tends to extend and flex the spine. Therefore, true seals are able to make progress over land by a method of locomotion similar to that used by some caterpillars. Extension and flexion of the body axis is coupled with alternate periods of grip and release of the substratum. Terrestrial locomotion is very probably an expensive pursuit for seals, requiring vigorous muscle contraction. Fortunately, gravity plays a relatively trivial role in the life of a true seal, so that static support of muscle bulk is probably not costly in itself. Perhaps it is not surprising that pinnipeds seem to spend a good deal of their terrestrial life dozing.

Slijper (1946) calculated the moments of resistance of the vertebral bodies [from beam

theory, the product of the transverse diameter (breadth) and the square of the sagittal diameter (height)] of many mammals. He found that the moments of resistance for true seals lay between values for the fully aquatic cetaceans and sirenians and values for the terrestrial carnivores. Clearly, passive joint resistance must also be affected by the presence or absence of soft structural tissue as well as end-point properties. Perhaps modifications in the basically carnivore vertebral column involved the loss of ligaments (especially ligamentum flavum) and the loss of disc integrity. The superspinous and interspinous ligaments in the dog and cat have been studied by Heylings (1980). He described them as weaker than homologous ligaments of human intervertebral joints. He did not comment on the ligamenta flava or the intervertebral discs. Certainly there were marked differences between the jaguar and seal joints studied here (see Fig. 5). The differences between the bending properties of the intervertebral discs were particularly pronounced, despite gross similarities in the appearance of the disc annulus lamellae and nuclei. The material composition and corresponding mechanical properties of these discs warrant further investigation.

This series of studies has demonstrated some of the sagittal bending properties of mammalian lumbar–lumbar and lumbosacral joints. The enhanced compliance of seal joints was suggested to be an adaptation to terrestrial locomotion in true seals. Two distinct mechanisms for resisting flexion moments in the terrestrial species were presented. Considering the available literature on flexion resistance in the intervertebral joints of other species, it was suggested that there may be a scale-dependent shift in material from elastin to collagen in order to accommodate the increasing demands of stiffness and strength, while maintaining some spinal mobility. This idea, appearing to transcend differences in posture, locomotor mode and taxonomic lineage, certainly warrants further study.

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