

Mammalian spinal biomechanics: postural support in seated macaques

Julianna Gal*

School of Applied Sciences, University of Glamorgan, Trefforest, Pontypridd CF37 1DL, Wales, UK

*e-mail: jgal@glam.ac.uk

Accepted 3 April 2002

Summary

The aim of this study was to investigate whether the ligamentous lumbar vertebral column of a macaque could potentially provide passive mechanical support to the weight of the head, upper body and forelimbs during upright sitting. The seated flexed curvature of the lumbar spine of *Macaca sylvana* was estimated from a photograph and was partitioned equally among the lumbar–lumbar intervertebral joints. This flexed curvature was compared with the hyper-extended profile of the unloaded excised ligamentous spine of a related species (*Macaca fascicularis*) and used to calculate changes in intervertebral angle from the unloaded excised state to the loaded *in vivo* state. Changes in intervertebral angle were then used to calculate the net flexion moment required to bend the spine from the unloaded curvature to the seated curvature. The moment arm of the ventrally displaced weight of the head, upper body and forelimbs was

estimated and used to calculate a corresponding net force. It was found that this force corresponded to approximately 18% of the total body weight of the 2.34 kg sample animal. This compares with a likely fractional body weight of approximately 30–40% for the head, upper body and forelimbs of these primates. Therefore, approximately half of the ventral flexion moment associated with the combined weight of the head, upper body and forelimbs during sitting in these animals may be supported by the passive mechanical properties associated with the ligamentous lumbar spine. This represents a potential means of relieving muscular effort and saving metabolic energy.

Key words: biomechanics, sitting, posture, spine, macaque, *Macaca* spp.

Introduction

During bouts of foraging and grooming, quadrupedal primates typically adopt a sitting-type posture in which the head and upper body are not supported by the forelimbs. While the forelimbs are occupied with the fine movements of food or parasite selection, the requisite postural support must be derived from components of the axial skeleton.

Most primates frequently use a seated posture and, indeed, many species have evolved specialised posterior pads, the ischial callosities, upon which they sit. The prevalence of sitting was investigated recently by McGraw (1998), who found that 60–90% of the total awake time of six sympatric species of Old World monkeys was spent during seated activities (feeding, socialising and resting). While there were some differences among species in terms of their activity-specific preference for sitting, McGraw (1998) demonstrates the high frequency of use of the sitting posture amongst primates.

If, in these animals, the seated posture is maintained exclusively by active muscular contraction, then an individual may incur an appreciable energetic cost. If, however, the mechanical requirements for postural support were met at least in part by the passive mechanical properties of connective tissue, then metabolic energy would be saved. The aim of this

report is to consider whether the ligamentous spine of a macaque (*Macaca fascicularis*) is capable of providing passive mechanical support for the combined weight of the head, upper body and forelimbs during sitting.

Materials and methods

Fig. 1 shows two Barbary macaques (*Macaca sylvana*) in a sitting posture. Macaques (and members of numerous other primate species) typically show a flexed spinal curvature during sitting (e.g. Woodward and Hare, 1988). Fig. 2 shows a tracing of an X-radiograph taken of the excised ligamentous lumbosacral spine of a 2.34 kg male macaque (*Macaca fascicularis*). In marked contrast to Fig. 1, the spinal curvature is reversed, or hyper-extended.

In this paper, an attempt is made to estimate the bending (flexion) moment required to alter the spinal curvature from the excised ‘unloaded’ condition (e.g. Fig. 2, hyper-extended) to the seated ‘loaded’ condition (e.g. Fig. 1, flexed). The corresponding force will then be calculated by using an estimate for the flexion moment arm. Finally, the calculated force will be compared with the likely proportional weight of the head, upper body and forelimbs.



Fig. 1. A photograph showing a typical example of the external dorsal curvature of seated macaques (*Macaca sylvana*). The flexed dorsal curvature of the animal on the right (the 'groomer') was used to estimate the approximate total flexion angle of the lumbar column from tangents drawn to the upper and lower lumbar regions (indicated schematically in Fig. 3). This total flexion angle was then partitioned equally amongst all the lumbar–lumbar intervertebral joints. This photograph was reproduced with the kind permission of the photographer (John Bracegirdle).

The calculations are based upon a 2.34 kg macaque (*M. fascicularis*) with the spinal dimensions of that shown in Fig. 2 sitting with the flexed spinal curve displayed by the 'groomer' animal in Fig. 1 (*M. sylvana*). The body morphologies of macaques are highly conserved so that an extrapolation of the spinal flexion curve from one species to another should not present a serious problem (e.g. Napier and Napier, 1967).

Gal (1993a) conducted cyclic bending (extension and flexion) experiments with ligamentous lumbar–lumbar and lumbosacral intervertebral joints from *M. fascicularis*. Negative exponential functions of the form:

$$\Delta\theta_{iv} = A(1 - e^{-B(M/m)}), \quad (1)$$

where $\Delta\theta_{iv}$ is the change in intervertebral angle from the unloaded excised state and M/m is the applied bending moment (M) normalised with respect to the total body mass (m) of the host animal from which the vertebrae were taken. For these data, physical meanings may be attributed to A and B . A can be thought of as the range of motion of a particular intervertebral joint (in either extension or flexion). B can be thought of as the compliance of the intervertebral joint. The larger the value of B , the greater the compliance in that the asymptotic range of motion of the joint (A) may be achieved with a relatively small normalised bending moment.

The negative exponential model parameters for *M. fascicularis* lumbar–lumbar intervertebral joints in flexion are shown in Table 1 (adapted from Table 2 in Gal, 1993a). The mean values of A and B for L1L2 to L5L6 are shown. These

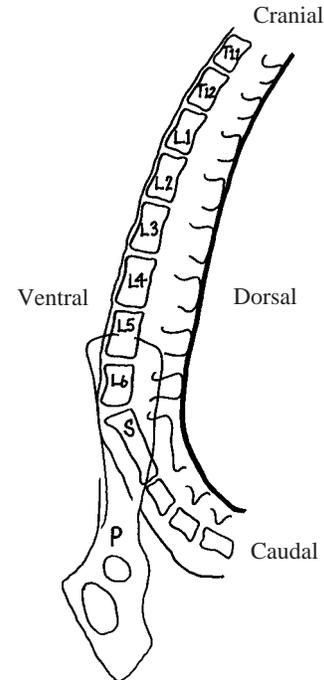


Fig. 2. A tracing of a sagittal X-radiograph of the lower thoracic and lumbosacral spine (excised, unloaded, ligamentous) of a 2.34 kg male *Macaca fascicularis*. In contrast to the *in vivo* dorsal curve during sitting (see Figs 1 and 3), here the lumbosacral spine is hyper-extended. P, S, L and T indicate the pelvis and the sacral, lumbar and thoracic vertebrae, respectively. The length of the lumbar column (L1–L6) is approximately 10 cm. The calculation in this study focuses on the lumbar column; the angles between these unloaded lumbar intervertebral joints were estimated by measuring the angles between lines drawn parallel to the long axes of the vertebral centra.

Table 1. The negative exponential model parameters for *Macaca fascicularis* lumbar–lumbar intervertebral joints in flexion (adapted from Gal, 1993a)

Joint and sample size (N)	A (degrees)	B (kg N ⁻¹ m ⁻¹)
L1L2 (16)	-16.1±1.00	6.0±1.9
L2L3 (17)	-12.3±0.99	2.6±0.8
L3L4 (13)	-14.5±1.83	2.4±1.1
L4L5 (13)	-11.4±0.61	3.7±1.4
L5L6 (14)	-10.3±0.63	19.2±6.7
Mean (L-L)	-12.9±1.10	6.8±3.2
L6S (15)	-23.1±1.56	4.2±1.6

The mean values of A and B (see equation 2 and text for definitions) for L1L2 to L5L6, inclusively, are shown (\pm S.E.M.). These mean values were used to construct a mean bending equation for macaque lumbar–lumbar (L-L) intervertebral joints in flexion.

The model parameters are also shown for the *M. fascicularis* lumbosacral joint in flexion (L6S) for comparison.

mean values were used to construct a mean bending equation for macaque lumbar–lumbar intervertebral joints in flexion. The model parameters are also shown for the *M. fascicularis* lumbosacral joint in flexion (L6S) for comparison. While *A* is notably greater for the lumbosacral joint compared with the lumbar–lumbar intervertebral joints, the values of *B* were similar across all macaque intervertebral joints relative to the magnitudes of their respective standard errors. This would suggest that, mechanistically, the lumbar–lumbar intervertebral joints are similar and, therefore, that generating a mean equation would seem to be reasonable. Therefore, the mean lumbar–lumbar flexion equation used in this study was:

$$\Delta\theta_{iv} = -12.9(1 - e^{-6.8(M/m)}). \quad (2)$$

The method for estimating the mean change in intervertebral angle from the unloaded excised state to the loaded *in vivo* state (during sitting) was as follows. The unloaded excised intervertebral angles were measured directly, from a tracing of the X-radiograph shown in Fig. 2, as the angles between lines drawn parallel to the long axes of adjacent vertebral centra (Gal, 1993a). The loaded *in vivo* angles were estimated from the external dorsal curve of the ‘groomer’ animal shown in Fig. 1. Dissections have shown that the spine of *M. fascicularis* lies very close to the dorsal surface and that spinous processes can be palpated along the external dorsal curve (Gal, 1993a). It was therefore assumed that the external dorsal curve was an accurate reflection of the internal spinal curve, as derived from the sum of the intervertebral joint angles along the length of the spine. Tangents were drawn to the external dorsal curve in the approximate regions of L1 and L6. The angle between these two tangents was estimated to be -20° (negative for flexion, as shown in Fig. 3), and was subsequently partitioned equally amongst all the lumbar intervertebral joints, giving flexion angles of -4° for each of the five joints. The change in intervertebral angle per joint was taken as the difference between the final angular position (flexed) and the initial

Table 2. The unloaded excised intervertebral angles were measured directly from a tracing of the X-radiograph shown in Fig. 2 as the angles between lines drawn parallel to the long axes of adjacent vertebral centra (Gal, 1993a)

Joint	Unloaded angle (degrees)	Loaded angle (degrees)	$\Delta\theta_{iv}$ (degrees)
L1L2	+6	-4	-10
L2L3	+3	-4	-7
L3L4	+4	-4	-8
L4L5	+3	-4	-7
L5L6	+7	-4	-11
Mean $\Delta\theta_{iv}$			-8.6 (≈ -9)

The loaded *in vivo* angles were estimated from the external dorsal curve of the ‘groomer’ animal shown in Fig. 1 (and explained in detail in the methodology text).

$\Delta\theta_{iv}$ per joint was taken as the difference between the loaded angular position (flexed) and the unloaded (hyper-extended) position.

angular position (hyper-extended). Since hyper-extended joint angles ranged from $+3$ to $+7^\circ$, changes in angle ranged from -7 to -11° , with a mean value of -8.6° (Table 2). This mean value was rounded up to the nearest degree, and thus -9° was substituted for $\Delta\theta_{iv}$ in equation 3, allowing the normalised net bending moment (*M/m*) to be calculated.

Results

Solving for *M/m* in:

$$-9 = -12.9(1 - e^{-6.8(M/m)}) \quad (3)$$

yields $0.176 \text{ N m kg}^{-1}$ which, when expressed in terms of the 2.34 kg animal, is approximately 0.41 N m. This is the net flexion moment required to bend the ‘average’ *M. fascicularis* lumbar–lumbar intervertebral joint through -9° from its unloaded, excised state.

Moments can be generated by an infinite number of combinations of force and moment arm. In the seated posture, the head, upper body and forelimbs of the macaque are

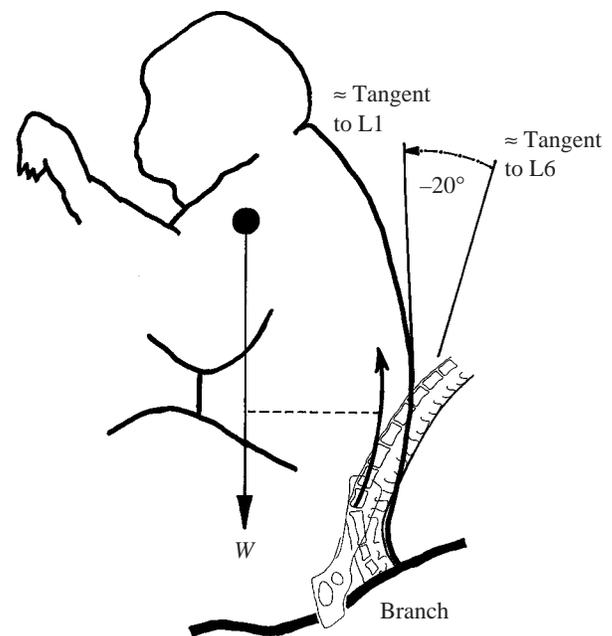


Fig. 3. An outline of the ‘groomer’ animal (from Fig. 1) with the lumbosacral X-radiograph (from Fig. 2) scaled down and superimposed to illustrate the contrast between the unloaded excised hyper-extended and the seated flexed, dorsal profiles. The length of the lumbar column (L1–L6) is approximately 10 cm. Tangents drawn to the approximate regions of L1 and L6 in the seated animal are shown, and the angle subtended, approximately -20° , was used to estimate the mean change in lumbar–lumbar intervertebral joint angle from the unloaded excised to the loaded *in vivo* state. The black circle indicates the approximate position of the centre of mass of the head, forelimbs and upper body in this particular seated posture. *W* is an estimate of the ‘weight’ of the collective head, upper body and forelimb masses, which exerts a flexion moment about the lumbar spine. The moment arm of *W* is indicated by the dashed line and is approximately 10 cm (0.10 m) in this animal.

displaced ventrally, relative to the spine, and therefore exert a flexion moment about the spine (see Fig. 3). This flexion moment is the product of the collective 'weight' of the ventrally displaced masses and the length of the moment arm. Since the lumbar column is oriented almost vertically, each lumbar–lumbar intervertebral joint 'sees' approximately the same moment arm because the line of action of the weight of the ventrally displaced head, upper body and forelimbs is approximately equidistant from each lumbar intervertebral joint centre. The length of the moment arm may be approximated by considering the location of the centre of the collective mass of the head, upper body and forelimbs, relative to the location of the intervertebral joint centres, in the sagittal plane. Thus, for a 2.34 kg animal with the vertebral dimensions shown in Fig. 2 (i.e. L1–L6 is approximately 10 cm) sitting with the same posture as the 'groomer' animal shown in Fig. 1, this flexion moment arm would also be approximately 0.10 m (see Fig. 3).

The net force associated with the net required bending moment to support the observed seated vertebral curvature would be equal to $0.41/0.10$ N, or 4.1 N. The total body weight of the 2.34 kg macaque is approximately 23 N; 4.1 N constitutes approximately 18% of that total. The fraction of the total body weight attributable to the head, forelimbs and upper body probably lies within the range 30–40% [estimated from data published by Vilensky (1979) and Preuschoft et al. (1998)]. This means that the passive support afforded by the flexed ligamentous lumbar spine constitutes approximately half the total support required to balance the spinal flexion moment exerted by the head, upper body and forelimbs in the seated posture exhibited by the 'groomer' animal in Fig. 1.

Discussion

The results of this study demonstrate that the ligamentous lumbar spine of *M. fascicularis* can provide a significant amount of passive mechanical support to the sitting posture by helping to counteract the flexion moment generated by the ventrally displaced head, forelimbs and upper body about the spine. For this particular calculation, the passive support so provided is approximately 50%.

The precise ventral bending moment that must be supported at any one time during sitting is highly variable. Slight changes in the position of the head and upper body, relative to the spine, can change the moment arm length of their collective weight and, hence, alter the ventral or flexion moment that must be supported. Perhaps more importantly, the instantaneous length of reach of the forelimbs can also change the flexion moment, particularly when one considers that primates tend to have elongated proximal limb segments containing muscles with long fibres (Alexander, 1985) and are therefore likely to be relatively heavy. More recently, Preuschoft et al. (1998) commented that both prosimian and simian species possessed relatively heavy hands and that there was little difference between the masses of the upper arms and forearms. These features give many primate species, including the macaques, relatively heavy upper limbs which, when significantly

displaced in the ventral direction relative to the spine, would exacerbate the flexion moment requiring support during sitting.

Thus, any amount of passive mechanical support from the ligamentous lumbar spine would be beneficial in terms of reducing the energetic cost of supporting the seated posture, particularly if the alternative was total support and control by selective activation of the axial musculature. However, it is possible that additional passive mechanisms may be invoked during sitting in these animals. For example, moments resisting excessive spinal flexion may be generated by abdominal compression. The present study was conducted to explore the potential for passive support by the ligamentous lumbar spine only, and comments on additional passive mechanisms at this time are purely speculative.

A passive spinal mechanism for the support of posture during sitting represents a potentially important energy-saving mechanism for macaques and possibly other primate species. They spend significant proportions of their waking hours occupied in grooming and foraging activities, both of which are performed primarily while seated (e.g. McGraw, 1998). While connective tissue structures, notably tendons, have been well documented with respect to their contribution to locomotor energetics (e.g. Alexander, 1988), the contribution of connective tissues to the energetics of posture have been less well documented. Dimery et al. (1985) have suggested that the nuchal ligament can function as a supporting spring for large bovids. Their experiments have shown that the weight of the head could be supported by strain in this robust, elastin-rich ligament, with a minimal requirement for muscle activation. Given that grazing is arguably the main activity performed by many bovids, passive head support must represent a significant energy-saving mechanism for these animals. It is possible that the ligamentous spine is working in a similar way in sitting macaques.

In a general sense, when the vertebral column is flexed, dorsal elements become subjected to tension, while ventral structures become compressed. Gal (1993b) demonstrated that, if the ligamentum flavum (the relatively robust yellowish dorsal intervertebral ligament connecting vertebral arches) was severed, the resistance to applied flexion moments was almost completely eliminated from the macaque lumbar–lumbar and lumbosacral joints studied. Thus, the integrity of the ligamentum flavum appeared to be of paramount importance to the function of the macaque spine in supporting flexion moments. At the same time, the relatively ventral intervertebral discs did not appear to offer any significant compressive resistance to the applied flexion moments, at least within the ranges of angular change evoked during the cyclic bending tests performed. While the angular changes selected for the cyclic bending experiments appeared to coincide with the maximum ranges of motion for each macaque intervertebral joint tested, it is possible that, during sitting, bending stresses occur in combination with additional compressive and/or torsional stresses. Quantitative information on the mechanical behaviour of non-human primate intervertebral joints subjected to combined stress protocols is unavailable at this time for comparison.

Therefore, it would appear that support of spinal flexion moments is manifest primarily by the collective strain in ligamenta flava throughout the vertebral column of the macaque. The yellowish tinge and permitted extension of these particular spinal ligaments suggest a relatively high elastin content. To support prolonged static loads, it is important for the structural material to be resistant to mechanical creep, that is, continued strain deformation under the application of a fixed prolonged stress. Vertebrate tendon, which is considered to be a near-pure source of collagen, has been shown to suffer creep damage (Wang and Ker, 1995). Elastin, however, is resistant to creep damage (Wainwright et al., 1976), which makes it a more suitable material for such a suspension-type mechanism of support. Elastin, however, is far less stiff and strong than collagen, so this type of passive supporting mechanism may have physical limits in terms of the absolute size of animal that can take advantage of a suspensory-type of spinal design. The possible influence of scale, in terms of the functional morphology of the primate spine, warrants further investigation.

The author sincerely wishes to thank both Professor R. McN. Alexander and Professor John Gosline for their valuable comments regarding the preparation of this manuscript. Additional thanks are due to the journal editor and two referees, whose constructive comments were helpful in producing the final published version.

References

- Alexander, R. McN.** (1985). Body size and limb design in primates and other mammals. In *Size and Scaling in Primate Biology* (ed. W. L. Jungers), pp. 337–343. New York: Plenum Press.
- Alexander, R. McN.** (1988). *Elastic Mechanisms in Animal Movement*. Cambridge: Cambridge University Press.
- Dimery, N. J., Alexander, R. McN. and Deyst, K. A.** (1985). Mechanics of the ligamentum nuchae of some artiodactyls. *J. Zool., Lond.* **206**, 341–351.
- Gal, J.** (1993a). Mammalian spinal biomechanics. I. Static and dynamic mechanical properties of intact intervertebral joints. *J. Exp. Biol.* **174**, 247–280.
- Gal, J.** (1993b). Mammalian spinal biomechanics. II. Intervertebral lesion experiments and mechanisms of bending resistance. *J. Exp. Biol.* **174**, 281–297.
- McGraw, W. S.** (1998). Posture and support use of Old World monkeys (Cercopithecidae): The influence of foraging strategies, activity patterns, and spatial distribution of preferred food items. *Am. J. Primatol.* **46**, 229–250.
- Napier, J. R. and Napier, P. H.** (1967). *A Handbook of Living Primates, Morphology, Ecology and Behaviour of Nonhuman Primates*. London: Academic Press.
- Preuschoft, H., Gunther, M. M. and Christian, A.** (1998). Size dependence in prosimian locomotion, and its implications for the distribution of body mass. *Folia Primatol.* **69** (Suppl. 1), 60–81.
- Vilensky, J. A.** (1979). Masses, centres-of-gravity and moments-of-inertia of the body segments of the Rhesus monkey (*Macaca mulatta*). *Am. J. Phys. Anthropol.* **50**, 57–66.
- Wainwright, S. A., Biggs, W. D., Currey, J. D. and Gosline, J. M.** (1976). *Mechanical Design in Organisms*. Princeton, NJ: Princeton University Press.
- Wang, X. T. and Ker, R. F.** (1995). Creep rupture of wallaby tail tendons. *J. Exp. Biol.* **198**, 831–845.
- Woodward, J. and Hare, T.** (1988). *The Illustrated Encyclopaedia of Wildlife*, vol. 14. London: Orbis Publishing Ltd.