Vertebral Bodies or Discs

Which Contributes More to Human-like Lumbar Lordosis?

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Abstract

Background The attainment of upright posture, with its requisite lumbar lordosis, was a major turning point in human evolution. Nonhuman primates have small lordosis angles, whereas the human spine exhibits distinct lumbar lordosis (30°–80°). We assume the lumbar spine of the pronograde ancestors of modern humans was like those of extant nonhuman primates, but which spinal components changed in the transition from small lordosis angles to large ones is not fully understood.

Questions/Purposes We wished to determine the relative contribution of vertebral bodies and intervertebral discs to lordosis angles in extant primates and humans.

Methods We measured the lordosis, intervertebral disc, and vertebral body angles of 100 modern humans (orthograde primates) and 56 macaques (pronograde primates) on lateral radiographs of the lumbar spine (humans—standing, macaques—side-lying).

Results The humans exhibited larger lordosis angles (51°) and vertebral body wedging (5°) than did the macaques (15° and –25°, respectively). The differences in wedging of the intervertebral discs, however, were much less pronounced (46° versus 40°).

Conclusions These observations suggest the transition from pronograde to orthograde posture (ie, the lordosis angle) resulted mainly from an increase in vertebral body wedging and only in small part from the increase in wedging of the intervertebral discs.

Introduction

Upright posture and bipedality are distinctive features of hominids and obvious adaptive departures from their pronograde living relatives [42]. The curvature of the lumbar spine in the sagittal plane (lumbar lordosis) is instrumental in maintaining upright posture because it stabilizes the upper body over the lower limbs in bipeds and allows the loads applied to the spinal column to be efficiently absorbed [16, 22, 55]. The degree of lordotic curvature exhibited by primates generally correlates with their mode of locomotion; in pronograde quadrupedal primates, the lordosis angles are small or nonexistent, whereas in orthograde bipedal primates, they are large (30°–80°) [1, 5, 24, 30, 43, 46, 53] with the exception of some lemur species, which exhibit orthograde posture and small lordosis angles [1, 35, 43, 46, 48].

Lumbar lordosis is formed by wedging of the lumbar vertebral bodies and intervertebral discs [24, 29, 44, 52]. Lordotic or dorsal wedging (ventral height greater than dorsal height) of the vertebral bodies and intervertebral discs increases the lordosis angle, whereas kyphotic or ventral wedging (ventral height less than dorsal height)

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decreases it. Increased dorsal wedging of the vertebral bodies is believed to have contributed to the increase in the lordosis angle in human evolution [1, 13, 32, 43, 45, 46].

The principal functions of the intervertebral disc are to anchor the vertebral bodies together, confer limited mobility on the spine, and act as a load-transmitting and shock-absorbing unit for body weight and muscular activity through the spinal column. The mechanical response of the intervertebral disc is dependent partially on its geometric parameters [12, 38, 50]. For example, lumbar intervertebral discs with dorsal wedging are at less risk for posterior disc bulge under pure axial compressive loading than are discs with ventral wedging [3, 15, 17], thereby protecting the spinal cord and cauda equina from compression.

The relative contributions of wedging of the bodies and discs to increased lordosis angles in hominids in the transition from pronograde and orthograde primates remain unclear. Therefore, the goals of this study were to: (1) compare lumbar lordosis angles of orthograde humans with those of pronograde macaques, (2) compare wedging of the lumbar vertebral bodies of orthograde humans with that of pronograde macaques, (3) compare wedging of the lumbar intervertebral disc of orthograde humans with that of pronograde macaques, and (4) determine the contributions of vertebral bodies and intervertebral discs in forming the lordosis angles of pronograde and orthograde extant primates and discuss the evolutionary relevance of the findings.

Materials and Methods

We examined lateral radiographs of the lumbar spine of 100 orthograde primates (modern humans) and 56 pronograde primates (macaques). The radiographs of the modern humans were used in a previous study [5], and the radiographs of the macaques came from the research collection of the University of Washington, Seattle, and from zoos and veterinary hospitals in Israel, where the radiographs were taken to detect health problems. The radiographs were selected according to the following criterion: adult subjects with no spinal fractures, scoliosis, or spondylolisthesis and minimal osteoarthritis. In all cases, we obtained standard lateral lumbar radiographs. Humans and macaques have a wide ROM of the lumbar spine in the sagittal plane [18, 19, 39, 51]; therefore, the posture in which the radiographs were taken is important to interpretation of the results. We chose to compare the two genera in a position as close as possible to their natural stance posture. The macaques were lying on their sides with naturally flexed shoulders and hips ($\pm 90^\circ$) and an unflexed lumbar spine in a position as relaxed and as close to their natural stance posture as possible (Fig. 1), similar to the position described by

Fig. 1 The lateral lumbar radiograph of an adult macaque is shown. The small lordosis angle of the macaque's spine is evident, especially compared with that of the human.

Preuschoft et al. [43]. The modern humans were standing in a comfortable position with the knees straight and arms folded across the chest.

Macaque monkeys (*Macaca* sp.) are medium-sized (5–20 kg), pronograde, terrestrial primates with a global distribution. We measured the spines of two species of macaques, *M. mulatta* and *M. fascicularis*. As the morphologic features of the spines of both species are well-characterized and we observed no differences between the species, we combined the values for all analyses. Macaques have been used as models of the human condition to study osteoporosis [10, 11], osteoarthritis [14, 31], and intervertebral disc mechanics [40]. Despite their use as models of human spinal biology, macaques are quadrupeds with little or no lumbar lordosis [1, 43]. Because of this, they have been used extensively as models to study the development and effects of facultative bipedalism on a naturally pronograde spine [25–28, 36, 37, 43]. Consequently, we use morphologic features of their spine as an exemplar of a generalized pronograde primate.

Because lordosis angle is dependent on the number of vertebrae included in the calculation [24, 53], and the normal number of lumbar vertebrae differs between modern humans (five) and macaques (seven) [23, 46, 48], standardization is required to compare results among the different primate genera. We used the number of lumbar segments found in modern humans, because previous studies that measured macaque lordosis angles chose to use five presacral segments in comparisons with human values [43]. Measuring more than five presacral segments reduces the lordosis angle of humans or macaques [43, 53]. We measured the body and disc angles for PS6 and PS7 in a

subsample of 20 macaques and found that the angles averaged over five presacral segments did not differ from those averaged over seven segments (data not shown). Thus, we chose to compare the lordosis formed by the five presacral segments. To facilitate comparison among the different primate groups, we numbered the vertebrae in relation to the sacrum, because others have compared the lumbar vertebrae of nonhuman primates and modern humans [1, 32]. The vertebra just above the sacrum is denoted PS₁ (first presacral) in all of the spines; the vertebra above it is denoted PS₂ and so forth.

Lordosis angle can be measured by numerous methods, including the Cobb method (Fig. 2); the vertebral centroid [8]; the TRALL–tangential radiographic assessment [9]; the tangent arc [52]; the Harrison posterior tangent [24]; and others [54]. The Cobb method (and its modifications) is widely used and considered the standard method for lumbar lordosis measurements [54]. Moreover, the few articles that have published direct measurements of lordosis angles of macaques [1, 25, 43] have used the Cobb method; therefore, we chose to use the Cobb method in our study.

All radiographs were assessed by one of us (EB). For each of the five presacral vertebrae, two lines were drawn (Figs. 2, 3): along the superior end plate of the cranial vertebral body and the inferior end plate of the caudal vertebral body. These lines were used to measure three angles: the lordosis angle (LA, Fig. 2) between the superior

Fig. 2 The method for measuring lumbar lordosis angle (LA) is shown on a lateral radiograph of an adult human. The human spine has a large lordosis angle, especially compared with that of the macaque.

end plate of PS₅ and superior end plate of S₁; the vertebral body wedge angle (B, Fig. 3) between the superior and inferior end plates of the same vertebral body; and the intervertebral disc angle (D, Fig. 3) between the inferior end plate of one vertebra and superior end plate of the next vertebra. Measurements B and D were taken for each of the five presacral segments. All measurements were taken using a 25-cm Jamar goniometer (Sammons Preston; Patterson Medical Products Inc, Bolingbrook, IL) with a 360°-scale in 1°-increments. Measurements B and D were used to calculate ΣB (the sum of the body wedge angles of the five presacral vertebrae) and ΣD (the sum of the intervertebral disc angles of these vertebrae). To assess intrarater reliability of LA, B, and D, six radiographs were measured twice 3 weeks apart. The intraclass correlation coefficients were > 0.95 ($p < 0.01$) for LA, B, and D.

We determined differences in lordosis angles, vertebral body wedge angles, and intervertebral disc angles between orthograde humans and pronograde macaques using the unpaired two-tailed Student's t-test. The LAs of humans and macaques were compared as were the ΣB , ΣD , and the B and D values for each vertebral level (PS₁–PS₅). We determined differences for B and D between different spinal levels (PS₁–PS₅) within genera (*Homo*, *Macaca*) using the paired two-tailed Student's t-test. We used SPSS

Fig. 3 The method for measuring segmental measurements (B, D) is shown on a lateral radiograph of an adult human, using the example of PS₃ D, intervertebral disc angle of the third presacral vertebra, and PS₂ B, vertebral body wedge angle of the second presacral vertebra. Lordotic wedging of the intervertebral disc can be seen.

(SPSS Inc, Chicago, IL) for all analyses. We determined the relative contribution of ΣB and ΣD to the increased LAs in humans by calculating their relative percentage.

Results

The LA of the humans ($51^\circ \pm 11^\circ$) was greater ($p < 0.0001$) than that of the macaques ($15^\circ \pm 10^\circ$) by 36° (Table 1).

The vertebral bodies of the modern humans we examined showed more lordotic wedging ($p < 0.0001$) than those of the macaques (Fig. 4). All macaque vertebral bodies and human vertebral bodies PS₅ through PS₃ show kyphotic wedging, whereas human PS₂ and PS₁ show lordotic wedging. In humans, the mean body wedge angles increased ($p < 0.0001$) between PS₅ and PS₂ (1° – 2° /level); between PS₂ and PS₁, the angle increased ($p < 0.0001$) by almost 6° . The macaques, however, showed no change in wedging of PS₅ through PS₃, with small increases ($p = 0.004$) for PS₂ (1° /level) and PS₁ (3° /level). The sum of the vertebral body wedge angles (ΣB) was larger ($p < 0.0001$) in humans ($5^\circ \pm 10^\circ$) than in the macaques ($-25^\circ \pm 16^\circ$) (Tables 1, 2).

In contrast to the differences in body wedging seen between humans and macaques, the species exhibited comparable intervertebral disc lordosis. The mean wedging of the five intervertebral discs of the macaques ranged from

$5^\circ (\pm 4^\circ)$ lordosis at the most cranial intervertebral disc (PS₅) to $11^\circ (\pm 6^\circ)$ lordosis at the most caudal one (PS₁). The mean wedging of intervertebral discs of the humans ranged from $6^\circ (\pm 3^\circ)$ at PS₅ to $12^\circ (\pm 4^\circ)$ at PS₁. Wedging of the intervertebral discs of the humans was not different than those of the macaques at PS₁, PS₃–PS₅. Only at PS₂ was wedging of the intervertebral discs of humans more lordotic ($p = 0.01$) than in macaques. The sum of the intervertebral disc angles (ΣD) of the humans ($46^\circ \pm 10^\circ$) was more lordotic ($p = 0.01$) than that of the macaques ($40^\circ \pm 15^\circ$) (Tables 1, 2).

On average, the lumbar lordosis angle of humans is 36° greater than the lumbar lordosis angle of macaques. The relative contribution of vertebral body wedging (ΣB) to the difference is 30° (83%) and the relative contribution of intervertebral disc wedging (ΣD) is 6° (17%).

Fig. 4 The vertebral bodies (B) of the modern humans showed more lordotic wedging ($p < 0.0001$) than those of the macaques. ▲ = modern human and ● = macaque. Angles greater than 0° indicate lordotic wedging, angles of 0° indicate no wedging, and angles smaller than 0° indicate kyphotic wedging.

Table 1. Lumbar spinal angles of modern humans and macaques*

Measurement	Modern humans [†]	Macaques [†]	p Value
N	100	56	
LA	51 ± 11 (24, 75)	15 ± 10 (–10, 34)	< 0.0001
ΣB	5 ± 10 (–23, 28)	-25 ± 16 (–52, 28)	< 0.0001
ΣD	46 ± 10 (22, 72)	40 ± 15 (–6, 69)	$= 0.01$

* Positive values indicate lordotic wedging; negative values indicate kyphotic wedging; [†] $\bar{x} \pm SD$ (minimum, maximum); LA = lordosis angle; ΣB = the sum of body wedge angles; ΣD = the sum of intervertebral disc angles.

Table 2. Lumbar spinal angles at each presacral level of modern humans and macaques*

Spinal level	Body wedging (B)			Intervertebral disc wedging (D)		
	Human [†]	Macaque [†]	p Value	Human [†]	Macaque [†]	p Value
PS ₅	-4 ± 3 (–11, 4)	-6 ± 4 (–18, 6)	< 0.0001	6 ± 3 (–2, 16)	5 ± 4 (–10, 17)	NS
PS ₄	-1 ± 3 (–8, 5)	-7 ± 4 (–14, 6)	< 0.0001	7 ± 3 (2, 15)	6 ± 5 (–5, 14)	NS
PS ₃	0 ± 3 (–10, 5)	-6 ± 4 (–15, 6)	< 0.0001	9 ± 3 (0, 19)	8 ± 5 (–4, 18)	NS
PS ₂	2 ± 3 (–7, 10)	-5 ± 5 (–12, 8)	< 0.0001	11 ± 4 (2, 20)	9 ± 5 (–1, 18)	$= 0.01$
PS ₁	8 ± 3 (0, 16)	-2 ± 5 (–15, 9)	< 0.0001	12 ± 4 (1, 23)	11 ± 6 (–2, 23)	NS

* Positive values indicate lordotic wedging; negative values indicate kyphotic wedging; [†] $\bar{x} \pm SD$ (minimum, maximum); NS = nonsignificant.

Discussion

The attainment of upright posture was a major turning point in human evolution, and lumbar lordosis is instrumental in maintaining this posture [42]. Pronograde quadrupedal extant primates, like macaques, have small lordosis angles, whereas orthograde bipedal primates, like humans, exhibit distinct lumbar lordosis [1, 43, 46]. Pronograde quadrupedalism likely was a habitual posture during the early stages of hominoid evolution [7, 21, 33, 35, 41]. Despite the well-established differences in lordosis angles between pronograde and orthograde primates, the way in which spinal components were involved in the transition from small lordosis angles to large ones is not fully understood. We, therefore, determined the relative contribution of wedging of the bodies and discs to increased lordosis angles in hominids in the transition from pronograde to orthograde primates.

The study design contains several potential limitations. First, the radiographs of the nonhuman primates were taken while the animals were anesthetized. Consequently, they were not in their habitual orientation to gravitational forces, but instead were lying on their sides. This position, however, was as relaxed and close to their natural stance posture as possible, similar to the position described by Preuschoft et al. [43]. Second, we acknowledge the LA of reclining nonhuman primates may not reflect the LA of these primates in their natural stance posture, some evidence suggests it does. Macaques trained to walk bipedally develop pronounced lordosis with similar LAs in orthograde and pronograde postures [25, 43]. The LA of modern humans in an upright posture is similar to that when supine [4] and the LA in supine humans is not influenced by differences (5°–10°) in the position of the legs [34]. The natural position we used was chosen as the standard for the University of Washington collection after examination of a pilot study of radiographs of the same monkeys in natural and (unnaturally) extended positions. Recently, we reexamined these pilot radiographs to measure LA and found full extension increases LA on average 2° from the natural position. Finally, the LA measured in the current study closely resembles previously published data (Table 3) of macaques [1, 43]. Third, we compared the spinal angles of humans only with those of macaques and without a wider comparison with other primate species poses. Measuring the spines of other pronograde terrestrial primates (such as *Papio*) might change our results, although there is no evidence to suggest this. Unfortunately the radiographs of other species were not available to us, and we found no related data in the literature. The question regarding whether our results will hold true for another terrestrial pronograde primate remains a topic for future study.

Table 3. Spinal angles of macaques*

Study	Species	Number	Method	Segments	Lordosis angle	ΣB	ΣD	Difference in LA between humans and macaques
Modified after Preuschoft et al. [43]	<i>Macaca fasciata</i> (free-living monkeys)	7	Modification of the Cobb angle	PS ₅ –S ₁	12 ± 10		Lordotic wedging	
Modified after Abitbol [1]	<i>Macaca fascicularis</i>	16	Cobb angle	PS ₃ –S ₁	14 ± 1			Humans are 25° more lordotic
Modified after Schultz [46]	<i>Macaca</i>		Ventral profile of the lumbar and sacral region		11			Humans are 51° more lordotic
Current study	<i>Macaca fascicularis</i> , <i>Macaca mulatta</i>	56	Cobb angle	PS ₅ –S ₁	15 ± 10	–25 ± 16	40 ± 15	Humans are 36° more lordotic

* Positive values indicate lordotic wedging; negative values indicate kyphotic wedging; LA = lordosis angle; ΣB = the sum of body wedging angles; ΣD = the sum of intervertebral disc angles.

Table 4. Spinal angles of modern humans*

Study	Number	Method	LA	ΣB	ΣD
Modified after Kimura et al. [29]	8	Cobb angle	53 ± 12	0	53
Modified after Vialle et al. [53]	300	Cobb angle	58 ± 11	6	50
Modified after Korovessis et al. [30]	100	Cobb angle, disc and vertebral body height index	52 ± 13	Lordotic wedging	Lordotic wedging
Modified after Chen [8]	16	Cobb angle	48 ± 11	-2	51
Current study	100	Cobb angle	51 ± 11	5 ± 10	46 ± 10

* Positive values indicate lordotic wedging; negative values indicate kyphotic wedging; LA = lordosis angle; ΣB = the sum of body wedge angles; ΣD = the sum of intervertebral disc angles.

Orthograde primates usually show high lordosis angles, whereas pronograde primates show small angles, with the exception of some lemur species, which exhibit orthograde posture and small lordosis angles [1, 35, 43, 46, 48]. As described by Schultz [46] and Abitbol [1], we found the LA of orthograde humans is greater (36°) than the LA of pronograde macaques (Tables 3, 4).

In agreement with published data, we found the sum of vertebral body wedge angles (ΣB) of humans (5° lordotic wedging) is 30° more lordotic than ΣB of macaques (25° kyphotic wedging) (Tables 1, 3, 4). The degree to which vertebral body shape responds to environmental loading remains to be determined. Preuschoft et al. [43] and Shi et al. [49] reported quadrupedal macaques trained to walk bipedally showed an increase in dorsal wedging of their lumbar vertebral bodies, but Nakatsukasa et al. [37] did not find a difference in wedging of the lumbar vertebral bodies between a single macaque trained for bipedalism and untrained macaques.

The wedging we observed of the intervertebral discs of humans resembles the wedging described in the literature [8, 29, 30, 53] (Table 4). The small differences between wedging of the intervertebral discs of humans and macaques, compounded with the similarity in the magnitude of the increase in intervertebral disc wedging along the lumbar spine of humans and macaques, initially was surprising to us. The load on the lumbar spine presumably is greater in humans than in quadrupeds owing to the biomechanical demands of erect posture [37, 42, 43]. The intervertebral discs transfer load from one vertebral body to the next, at the same time allowing for spinal flexibility, roles that expose the discs to considerable mechanical demands [47, 50]. In bipedal locomotion, the entire weight of the upper body must be supported through the lumbar discs, whereas in quadrupedal locomotion, some weight is borne by the forelimbs. Static body weight, however, is not the only component of disc loading. Muscle activation and motion generate considerable compressive, tensile, and shear stress and strain in the tissue [2, 47, 50]. Although the load on the spine of small pronograde primates is much lower than that of humans,

their intradiscal pressure might be similar because the diameter of their discs on which this force is acting is much smaller [2]. Consequently, macaque intervertebral disc loading might be comparable to that of humans.

Dorsal wedging of the lumbar intervertebral discs decreases the risk of posterior disc bulging under pure axial compressive loading, whereas ventral wedging increased the bulge [3, 15, 17]. Because posterior and posterolateral disc herniations can impinge on the spinal cord and spinal nerve roots, causing substantial neurologic impairment, the enhancement of posterior disc integrity may confer protection from herniation. If in the course of evolution, however, the posterior margin of the intervertebral discs became very thin, as would be required for the discs to contribute to lumbar lordosis, the ROM between adjacent vertebrae could have been diminished and the ability to withstand compressive and torsional loads altered [6, 8, 20, 29].

Vertebral body wedging contributed 30° (83%) to the overall difference in LA between pronograde macaques and orthograde humans, whereas intervertebral disc wedging accounted for only 6° (17%) of the overall difference. This difference between extant primate genera might indicate that, in the transition from pronograde to orthograde posture, the increase in the LA resulted mainly from changes in the shape of the vertebral bodies and only in a small part from the increase in wedging of the intervertebral discs. Fossilized lumbar vertebrae rarely are found, so little is known about the lumbar morphology of hominid species that existed before the genesis of genus *Homo*. The only PS₁ vertebrae known from australopithecines (STW-14a and STW-431, *Australopithecus africanus*) exhibits lordotic vertebral body wedging in the human range [45, 55], but this is unsurprising given australopithecines were habitual terrestrial bipeds. The vertebral body wedging in older hominids or protohominids is unknown, although that of mid-Miocene hominoids like *Moroto bishopi* appears kyphotic [36]. Vertebral bodies seemed to have changed from the kyphotic wedging (as seen in macaques) to the lordotic wedging typical of modern humans early in the transition from pronograde to orthograde locomotor posture.

Our data show the larger lumbar LA of modern humans relative to macaques arises mainly from vertebral body wedging and in small part from wedging of the intervertebral discs. If this difference between extant primates with different locomotor regimes is reflective of the transition in locomotion style during human evolution, erect posture may leave an accurate record in lumbar vertebral bodies. The similarity in wedging of intervertebral discs of humans and macaques suggests some similarity between the mechanical demands placed on the presacral spines of the two species, further supporting the use of macaques as models of the human condition. The fact that symmetric disc shape is maintained in the presence of the substantial selective pressure for lumbar lordosis in humans suggests intervertebral disc integrity is of paramount importance.

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