

Kinematic Data on Primate Head and Neck Posture: Implications for the Evolution of Basicranial Flexion and an Evaluation of Registration Planes Used in Paleoanthropology

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ABSTRACT Kinematic data on primate head and neck posture were collected by filming 29 primate species during locomotion. These were used to test whether head and neck posture are significant influences on basicranial flexion and whether the Frankfurt plane can legitimately be employed in paleoanthropological studies. Three kinematic measurements were recorded as angles relative to the gravity vector, the inclination of the orbital plane, the inclination of the neck, and the inclination of the Frankfurt plane. A fourth kinematic measurement was calculated as the angle between the neck and the orbital plane (the head-neck angle [HNA]). The functional relationships of basicranial flexion were examined by calculating the correlations and partial correlations between HNA and craniometric measurements representing basicranial flexion, orbital kyphosis, and relative brain size (Ross and Ravosa [1993] *Am. J. Phys. Anthropol.* 91:305-324).

Significant partial correlations were observed between relative brain size and basicranial flexion and between HNA and orbital kyphosis. This indicates that brain size, rather than head and neck posture, is the primary influence on flexion, while the degree of orbital kyphosis may act to reorient the visual field in response to variation in head and neck posture. Regarding registration planes, the Frankfurt plane was found to be horizontal in humans but inclined in all nonhuman primates. In contrast, nearly all primates (including humans) oriented their orbits such that they faced anteriorly and slightly inferiorly. These results suggest that for certain functional craniometric studies, the orbital plane may be a more suitable registration plane than Frankfurt "Horizontal." *Am J Phys Anthropol* 108:205-222, 1999.

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Humans have a highly flexed cranial base. This unusual feature has been linked to other unusual human features, most notably brain enlargement and orthograde posture. Hypotheses relating basicranial form to brain size date back to the early part of this century (e.g., Bolk, 1926a,b). The premise of all brain-size hypotheses is that because the cranial base is also the floor of the cranial cavity, brain size is a fundamen-

tal constraint on basicranial form. As species evolve to have larger brains, the bones of the cranial base must reorganize to accommodate a larger organ (Moss, 1958; Du Brul

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and Laskin, 1961; Biegert, 1963; Vogel, 1964; Enlow, 1976, 1990; Riesenfeld, 1969; Gould, 1977). These modifications provide the solution to what Ross and Ravosa (1993:307) call the "spatial-packing" problem caused by the brain.

Recently, Ross and Ravosa (1993) demonstrated significant correlations between flexion and a measure of brain volume relative to basicranial length across a broad sample of primate species. Ross and Henneberg (1995) further found that, relative to other primates, humans have less flexed basicrania than would be expected given their relative brain size. They suggest that the cranial base is structurally constrained such that the angle between the clivus and presphenoid planes cannot fall much below 90° and cannot exceed 180° (i.e., that the relationship between brain size and flexion may be logistic rather than linear [more information is available in a new article submitted by Ross et al.]). Ross and Henneberg (1995) argue that the lower limit of 90° was attained early in human evolution, as demonstrated by *Australopithecus africanus*, precluding further flexion in response to increases in brain size. Subsequent increases in brain size were thereafter accommodated by changes in other aspects of cranial form (e.g., a high, rounded cranial vault). Spoor (1997) has recently questioned whether the brain size–flexion relationship is logistic, but his disagreement focuses on only a single species (*Homo sapiens*). With respect to other primates, his study corroborates the finding that relative brain size is related to flexion.

One implication of these conclusions is that the evolution of orthograde posture had little to do with the evolution of basicranial flexion among hominids. This argument was made by Ross and Ravosa (1993) on the basis of a simple nonparametric test of the hypothesis that orthograde primates have more flexed basicrania than pronograde ones. However, Ross and Ravosa's (1993) study suffered from a lack of quantitative data on head and neck posture. They defined orthograde posture qualitatively such that orthograde species were those that habitually employed orthograde body postures while sitting, standing, or locomoting (e.g., leap-

ers, brachiators). This behavioral classification is imprecise because body posture (the orientation of the trunk relative to gravity) is not directly relevant to basicranial morphology, insofar as the trunk does not articulate with the skull. Consequently, animals with orthograde body posture can nonetheless display pronograde neck posture (e.g., indriids). Rather, when discussing the postural hypothesis, the relevant measure of posture is either neck posture (the inclination of the neck relative to gravity) or the orientation of the head relative to the neck. Although some data on primate head and neck posture exist (Vidal et al., 1986; Graf et al., 1995a,b), they cannot easily be applied to studies of comparative primate anatomy because they have been collected on only a few species (*Macaca fascicularis*, *M. mulatta*, *Saimiri sciureus*, *Cebus apella*, *Homo sapiens*). The limited taxonomic scope of these studies reflects the fact that they employed methodologies (radiography, cineradiography) that can be applied only under laboratory conditions. Moreover, these studies did not collect data on primates during locomotor behaviors. Given that body movements during locomotion tend to be highly repetitive and that the entire skeleton may experience higher loads during locomotion than at rest, it is reasonable to suspect that head and neck postures during locomotion may be particularly relevant to studies relating posture to cranial form.

The present study aimed to rectify these deficiencies by collecting quantitative data on head and neck posture in living primates and using this data to test the relationships between relative brain size, head and neck posture, and cranial base flexion. We employed methods that, while necessarily less precise than those used by Vidal et al. (1986) and Graf et al. (1995a,b), allowed a greater sampling of primate species as well as the collection of postural data during locomotion.

In addition, this study sought to evaluate registration planes used in paleoanthropological analyses. The Frankfurt plane is widely used in such studies, principally because humans are known to hold this plane in a roughly horizontal orientation during habitual postures (Downs, 1952). Although

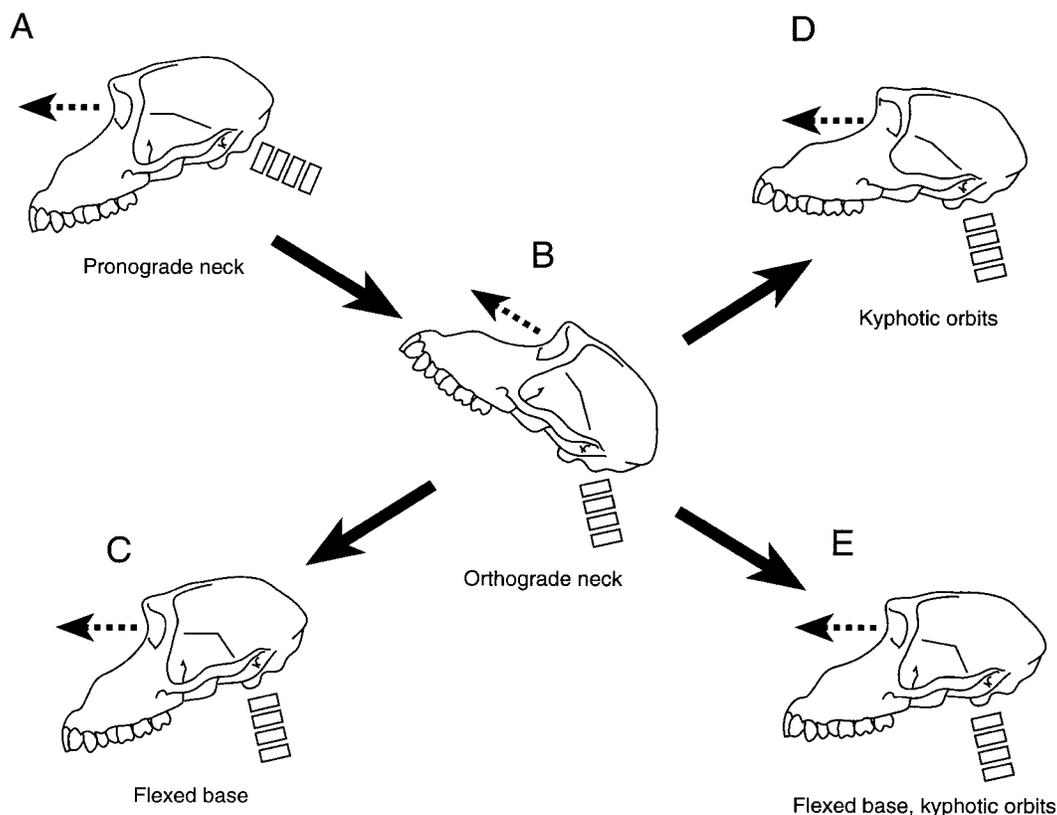


Fig. 1. Relationships between head posture, neck posture, basicranial flexion, and orbit frontation. **A:** Primate with pronograde neck posture, an anteriorly directed visual field, and an unflexed base. **B:** Primate in orthograde neck posture but without morphological alterations allowing it to maintain an anteriorly directed visual field. Three possible alterations include a flexed base (C), kyphotic orbits (D), and a flexed base and kyphotic orbits (E). Figure after Ross (1995).

this plane was designed to be used only in studies of humans (e.g., Enlow, 1990; Merow and Broadbent, 1990), it has been extensively applied to studies of early hominids (e.g., Tobias, 1967, 1991; Kimbel et al., 1984; Kimbel and White, 1988; Aiello and Dean, 1990; Luboga and Wood, 1990; Wood, 1991; Grine et al., 1993, 1996; Strait et al., 1997). Moreover, insofar as such studies employ measurements of nonhuman primates, it has been applied to those species as well. Even nonpaleontological studies have used the Frankfurt plane to characterize primate head posture (Vidal et al., 1986; Graf et al., 1995a,b). The influence of Frankfurt Horizontal is so pervasive that it affects morphological interpretations in studies that do not even name it explicitly. For instance, whenever a relatively complete fossil hominid

skull is described, it is conventional to depict it in the Frankfurt plane and to characterize its morphology accordingly (e.g., Walker et al., 1986; Kimbel et al., 1994). Unless fossil hominids and nonhuman primates hold this plane in a horizontal orientation (like humans), the data collected using this plane will be arbitrary and thus of questionable significance.

HYPOTHESES

Basicranial flexion

The premise of the postural hypothesis is that as primate species evolve from being pronograde (Fig. 1A) to being orthograde (Fig. 1B), they must maintain an anteriorly directed visual field. There are several ways to achieve this. The first is simply to have a

very flexible neck. This is an appropriate null hypothesis for theories attempting to relate posture to cranial morphology, for, if postural changes are not accompanied by morphological adaptations of the skull, they must be accommodated via morphological changes or behavioral adaptations in the neck.

Another solution is to flex the cranial base as the neck becomes upright, thereby maintaining the orbits in a roughly vertical orientation (Wood Jones, 1917; Weidenreich, 1924, 1941; Ross, 1995) (Fig. 1C). According to Weidenreich (1941:424),

the base of the human skull is deflected at the junction of pre- and postsphenoid so that the anterior part of the base is bent downwards. This skull "kyphosis" counterbalances the "lordosis" of the cervical portion of the spine. It brings the face down in adaptation to the new direction of locomotion which otherwise would have been looking upwards had it preserved its original orientation to the spine.

Under this hypothesis, flexion is dependent on and should be correlated with the orientation of the orbits relative to the neck.

Dabelow (1929) suggested an alternative solution in which the orbits of primates become kyphotic, meaning that the orbits are rotated ventrally on the skull (Fig. 1D). According to this hypothesis, orbital kyphosis, not basicranial flexion, should be correlated with an anteriorly directed visual field and an orthograde neck.

Dabelow (1929) also suggested that that both flexion and orbital kyphosis will occur in those species with highly approximated orbits (presumably because the anterior cranial base and upper face are structurally contiguous in these species). This hypothesis predicts that both flexion and frontation will be correlated with head and neck posture in species such as haplorhines and in particular cercopithecines (Fig. 1E).

The plausibility of the postural hypothesis is strengthened by recent observations that primates exhibit a restricted range of motion at the atlanto-occipital joint (Graf et al., 1995a). This suggests that primates cannot compensate for the inclination of the neck merely by reorienting their heads, perhaps necessitating some form of a morphological adjustment.

Registration planes

We also tested the validity of the Frankfurt Horizontal as a reference plane for craniometric research into morphological correlates of postural differences. Obviously, all registration planes exert considerable influence on the results of a morphological analysis, and for that reason some researchers (for review see Cole, 1996; Moss et al., 1987) have turned to methods that do not require such a plane (e.g., Euclidean distance matrix analysis [Lele, 1991, 1993; Lele and Richtsmeier, 1991, 1995; Lele and Cole, 1995, 1996]). However, certain research questions can be addressed only by employing a registration plane. For instance, the biomechanical significance of certain features (e.g., the effect of nuchal plane inclination on the mechanical advantage of the nuchal muscles) can be understood only in reference to the gravity vector, because the weight of an object or the torque imposed by its center of mass may be important biomechanical parameters. For such studies, a registration plane that exhibits a fairly consistent angular relationship with the gravity vector is desirable.

In general, a registration plane can be used if it exhibits a functional, structural, or developmental property that is consistent across all of the taxa being studied. If this property is not constant across taxa, the resulting data will be tainted with a registration artifact, which is essentially a bias introduced by the plane that does not reflect the functional or structural parameter for which the measurement was designed. In the case of the Frankfurt plane, the property in question is head posture, as indicated by the fact that many studies of the biomechanics and physiology of head balance have employed the Frankfurt plane (e.g., Schultz, 1942; Ashton and Zuckerman, 1951, 1952, 1956; Adams and Moore, 1975; Luboga and Wood, 1990; Graf et al., 1995a,b). Because nonhuman primates are often used as comparative samples with which to interpret human morphology, this plane would be suitable for representing habitual head posture if it was oriented similarly in human and nonhuman primates. If so, then presumably the Frankfurt plane would likewise

TABLE 1. Summary statistics for kinematic measurements¹

Species	Data collection condition	Substrate	Mode	Inclination Frankfurt plane			Inclination orbital plane			Inclination neck		
				N	Mean	SD	N	Mean	SD	N	Mean	SD
<i>Eulemur fulvus</i>	S	W beam	Quad	3	52.9	16.6	3	17.3	4.0	11	88.3	9.0
<i>Lemur catta</i>	S	Ground	Quad	26	61.4	7.4	24	5.0	5.1	28	88.7	9.5
<i>Varecia variegata</i>	S	W beam	Quad	4	64.5	4.0	6	6.2	7.7	13	91.7	10.6
<i>Alouatta seniculus</i>	S	W beam	Quad	29	54.6	10.9	26	21.0	7.2	33	107.6	6.9
<i>Ateles fusciceps</i>	S	Cage flr	Quad	2	63.3	1.2	19	11.9	4.7	25	75.1	7.3
	S	Ir beam	Brach	21	66.6	13.7	28	11.4	10.6	10	62.8	6.6
<i>Ateles geoffroyi</i>	S	Ground	Quad	6	67.7	6.3	10	10.9	10.6	10	62.8	6.6
	S	Ir beam	Brach	8	74.9	10.9	19	1.5	15.8	11	50.5	9.2
<i>Cebus apella</i>	S	W log	Quad	56	77.0	8.2	52	13.1	6.4	38	61.1	6.2
<i>Lagothrix lagothricha</i>	S	Cage flr	Quad	21	65.4	7.6	21	18.5	5.8	29	89.0	8.2
	S	Ir beam	Brach	22	79.8	9.6	29	11.3	6.3	24	63.1	8.6
<i>Saguinas mystax</i>	S	Cage flr	Quad	10	73.2	6.6	9	11.0	5.8	22	70.9	7.5
<i>Saimiri sciureus</i>	S	W log	Quad	42	75.6	4.8	41	10.8	4.9	40	48.5	12.0
<i>Cercopithecus aethiops</i>	S	W beam	Quad	19	68.2	9.9	24	17.8	8.0	27	58.7	6.6
<i>Cercopithecus albogularis</i>	S	W beam	Quad	2	57.9	0.9	18	23.9	7.6	39	90.0	8.2
<i>Cercopithecus diana</i>	S	Ir beam	Quad	31	56.2	11.2	24	16.1	9.2	39	73.1	9.7
<i>Cercopithecus mona</i>	S	W beam	Quad	26	55.4	9.8	29	22.6	10.4	38	70.4	5.7
<i>Cercopithecus petaurista</i>	S	W beam	Quad	44	62.9	8.0	40	18.5	9.5	43	70.3	8.9
<i>Erythrocebus patas</i>	C	Ground	Quad	26	72.9	10.7	26	12.3	9.5	26	53.6	5.1
	C	W beam	Quad	23	67.0	6.8	23	25.2	8.5	25	55.1	6.4
<i>Macaca fascicularis</i>	S	W beam	Quad	36	70.6	6.0	35	10.9	5.3	34	62.0	5.8
<i>Macaca fuscata</i>	S	Ground	Quad	25	84.6	11.7	27	2.1	10.7	20	51.8	8.1
<i>Macaca mulatta</i>	S	W beam	Quad	33	61.9	10.3	33	16.9	9.4	27	57.2	8.1
<i>Papio hamadryas</i>	S	Cage flr	Quad	13	60.5	18.0	22	19.6	9.6	20	58.4	6.1
<i>Papio ursinus</i>	U	Ground	Quad	17	71.0	8.2	16	11.2	7.8	18	61.9	5.6
<i>Colobus angolensis</i>	S	W beam	Quad	7	49.8	12.8	18	19.5	6.9	21	70.1	10.4
<i>Colobus guereza</i>	S	Ir beam	Quad	17	55.7	9.5	16	25.7	6.7	18	71	11.3
	S	Ir beam	Leap	23	49.1	5.6	17	27.7	6.1	23	89.9	6.4
<i>Hylobates lar</i>	S	Ir beam	Brach	59	82.1	13.9	40	2.0	9.7	53	47.0	9.7
<i>Symphalangus syndactylus</i>	U	W beam	Brach	9	80.6	10.6	10	-11.6	4.8	2	49.7	3.7
<i>Pongo pygmaeus</i>	U	C beam/rope	Susp	24	75.0	28.4	43	17.1	37.2	47	55.0	28.9
<i>Gorilla gorilla</i>	S	Ground	Knuck	20	59.6	11.2	31	18.4	5.3	33	56.4	6.0
<i>Pan troglodytes</i>	U	Ground	Knuck	45	49.2	12.2	47	23.4	7.8	54	81.5	8.0
<i>Homo sapiens</i>	C	Ground	Biped	28	93.2	3.1	28	9.3	5.7	44	17.9	7.3

¹ Data collection conditions: C, controlled; S, semicontrolled; U, uncontrolled. Substrates: C beam, cement beam; Cage flr, cage floor; Ir beam, iron beam; W beam, wooden beam; W log, very thick wooden beam. Mode of locomotion: Biped, bipedalism; Brach, brachiation; Knuck, knuckle-walking; Leap, quadrupedal leaping; Quad, quadrupedalism; Susp, quadrumanous suspension.

have been similarly oriented in fossil hominids. But if humans and nonhuman primates differ, then the possibility exists that fossil hominids might not have oriented the plane in a human-like fashion.

MATERIALS AND METHODS

Subjects

To test these hypotheses, we collected data on head and neck posture from adult representatives of 29 species of primates (Table 1), took measures of basicranial flexion and orbital kyphosis from lateral radiographs of skulls representing these same 29 species, and also took a measure of relative endocranial volume from the same skulls.

Postural measures

Three kinematic measures of head and neck posture were taken from video images of primates filmed during locomotion: the inclination of the neck, the inclination of the orbital plane, and the inclination of the Frankfurt plane. The inclination of the orbital plane was measured as the angle relative to the gravity vector of the line joining the superior and inferior margins of the orbits. Neck posture was measured as the inclination of the dorsal surface of the neck relative to gravity. A similar measurement was found to be significantly (but weakly) correlated with the inclination of the cervical vertebral bodies in an intraspecific sam-

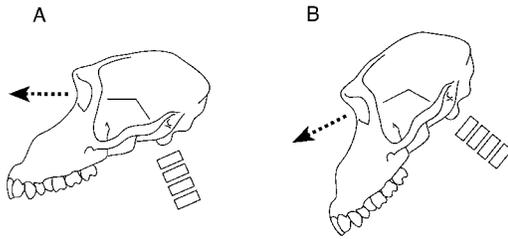


Fig. 2. Basicranial flexion and the interaction between head and neck posture. **A:** Primate in orthograde posture with an anteriorly directed visual field. **B:** Primate in more pronograde posture with an inferiorly directed visual field. In both A and B, the angular relationship between head and neck posture is equivalent, resulting in equivalent degrees of basicranial flexion.

ple of humans (Refshauge et al., 1994). Because the inclination of the cervical vertebrae was not measured directly, the neck posture data presented here should be considered approximate. In order to test the validity of the Frankfurt "Horizontal" as a measure of head posture, the inclination of the line infraorbitale–porion relative to gravity was measured.

A fourth measure of posture was calculated that reflects the orientation of the head relative to the neck. This final measurement is the critical one needed to evaluate hypotheses relating differences in posture to differences in basicranial flexion. Consider a case in which a primate species habitually holds its orbits in a nearly vertical orientation and its neck in orthograde posture (Fig. 2A). Because the basicranium is a structural interface between the neck and head, this species is expected to display, among other features, an internally flexed cranial base. Now consider a species that has a more pronograde neck posture but that habitually inclines its orbits so they face more inferiorly (Fig. 2B). Despite the fact that the latter species has a more horizontally inclined neck, both species exhibit an equivalent degree of basicranial flexion. The reason for this is that the relative orientations of the orbits and neck in both species are equivalent. Thus, the relative inclinations of the orbital aperture and the neck must be measured. Such a measure, the head-neck angle (HNA), was obtained by subtracting the mean value for orbit inclination from the

mean value for neck inclination for each species. Ideally, HNA would be calculated by subtracting orbit inclination from neck inclination for each video image that was digitized, but this was impractical because it was often the case that only one of the two measures could be taken on a given video image.

Postural data were collected by filming living primates during locomotion and then digitizing the images on a computer and extracting angular measurements using MacMorph software (Spencer and Spencer, 1993, 1995). Our data do not capture the full range of head and neck movement. In particular, no attempt was made to collect data when subjects were at rest, as preliminary observations suggested that resting animals hold their heads and necks in a wide variety of positions. Although resting postures may be significant influences on basicranial form, it is noteworthy that subjects employed a much more restricted repertoire of head and neck postures during locomotion, suggesting that head and neck posture during locomotion may be under stricter selective control than during resting.

Postural data were collected under three types of conditions: controlled or laboratory conditions, semicontrolled or zoo conditions, and uncontrolled or wild conditions. Under controlled conditions, subjects were shaved, and colored cotton markers were affixed (glued) to points on the skin overlying craniometric and cervical landmarks (inion, glabella, infraorbitale, supraorbitale, porion, spinous process C2, spinous process C7). Subjects were then coaxed, using food rewards, to move back and forth along a known path. As they moved, the primates were simultaneously filmed in lateral and superior view. A laterally placed (high resolution) camera was positioned such that it was perpendicular to the expected path of the subject, and it was this camera that provided video images from which kinematic data were collected. A plumb bob was suspended in the background to indicate the gravity vector. Frames in which the subject's forelimb was in either midstance or mid-swing were selected for digitization (mid-swing refers to the middle of the swing cycle

of suspensory locomotion, not the swing phase of a step cycle). However, suitable kinematic data could be obtained only when the magnification of the camera was set such that the head and neck filled the screen. Thus, the timing of midstance and midswing could only be approximated.

A superiorly placed (standard resolution) camera was positioned above the expected path of the subject and was used to select frames in which the head and neck were perpendicular to the main camera. *Perpendicular* was defined as the state in which the long axes of the head (glabella-inion) or neck (spinous processes of C2–C7) were within 15° of the line indicating the expected path of the subject. Note that C2 and C7 were not used as landmarks for the collection of neck inclination data but were used only to assess the deviation of the neck from the axis perpendicular to the laterally placed camera. Neck inclination was measured along the flattest surface of the dorsal aspect of the neck. This was necessary in order to make the data collected under controlled conditions comparable to those collected under other conditions and because primate species exhibited variability as to the inclinations of different portions of their necks. Qualitatively, neck inclination was most often measured between approximately C2 and C5.

Under semicontrolled conditions, subjects were neither shaved nor marked. Hair was an important confounding factor, but most of the species filmed under these conditions had neck hair that was short or of only moderate length. Filming conditions varied somewhat among species because of the unique constraints imposed by the cages or enclosures in which each species was filmed. In general, subjects were filmed with a laterally placed camera, and a leveling tool was used to ensure that the camera was mounted in the horizontal plane. Thus, the vertical axis of the screen was used to approximate the gravity vector. As before, subjects were filmed simultaneously in two views, but, instead of being filmed from above, they were filmed with a camera that was positioned along the axis of their expected path (i.e., a camera that filmed sub-

jects from either the front or the back, depending on the direction in which the subject was moving). The axial camera served the same purpose as the superiorly placed camera, to select frames for digitization, but the selection process was qualitative rather than quantitative.

Under uncontrolled conditions, subjects were neither shaved nor marked, and they were filmed from an approximately lateral position. Subjects were not coaxed using food rewards, and thus they were filmed opportunistically. Only one camera was used to film the primates, and it was held in an approximately horizontal orientation.

Most species were filmed during quadrupedal locomotion, although some were filmed during brachiation, quadrupedal leaping, quadrumanous suspension, knuckle-walking, and bipedalism. Four species engaged in two modes of locomotion (*A. geoffroyi*, *A. fusciceps*, *L. lagotricha*, *C. guereza*). Quadrupeds, bipeds, and knuckle-walkers were filmed during walking gaits. Brachiators were filmed during slow brachiation (i.e., the subject always had at least one limb grasping a support). Quadrupedal leaps were of short distance and between horizontal supports. Certainly faster or more dynamic gaits may be important selective factors affecting posture and cranial morphology, but the enclosures in which most of the subjects were filmed generally did not allow such gaits; by the time a subject accelerated to a running gait, it would exhaust the available space and have to slow down. The number of observations for each measurement varied widely among and sometimes within species, largely due to the varying conditions under which the species were filmed (e.g., lighting, configuration of cages), the degree to which the subjects cooperated with the experiment, and the clarity of the video images. With respect to most species, the subjects were separated from the cameras by a chain-link cage wall, which often had the effect of obscuring cranial or cervical landmarks on the video images. As a result, the final sample sizes represent only a fraction (about 20–50%) of the number of times that a subject passed in front of the laterally placed camera.

Craniometric measures

Data on the degree of basicranial flexion, orbital kyphosis, and relative brain size were obtained for the same 29 species for which postural data were gathered. The degree of basicranial flexion was measured using the cranial base angle (CBA), which is calculated as the angle between the clivus and presphenoid planes. This measure sums the pre- and postsella flexions observed in primates and other mammals (Moss and Vilman, 1978). Note that flexion increases as the angle decreases. The degree of orbital kyphosis was measured using the angle of orbital axis orientation (AOA), calculated as the angle between the clivus and the axis passing from the optic canal through the center of the orbits. Relative brain size was measured using the index of relative encephalization (IRE), calculated as the cubed root of neurocranial volume divided by basicranial length (BL). BL reflects a series of chord distances taken along the midline endocranial contour of the basioccipital, basisphenoid, and presphenoid. Formal definitions of these measurements can be found in Ross and Ravosa (1993), and most of these data were taken from Ross (1993), Ross and Ravosa (1993), and Ross and Henneberg (1995). Additional data were gathered for species not represented in those studies.

It is worth emphasizing the distinction between two types of orbital orientation measurements. *Orbit inclination* refers to a kinematic measure of head posture, specifically the direction in which the orbits face when the head is held in habitual postures. *Orbital kyphosis* is a craniometric measure of how the orbits are positioned within the skull (Ross and Ravosa, 1993).

Statistical analyses

The hypotheses were evaluated by computing Pearson's product-moment correlations ($P < 0.05$) for all bivariate comparisons between HNA, IRE, CBA, and AOA. In addition, partial correlation analyses ($P < 0.05$) were carried out to isolate that portion of the total variance in CBA associated with one variable while controlling for correlations with other independent variables. In all bivariate comparisons, humans were out-

liers. Because outliers can have an undue influence on statistical tests, correlations and partial correlations were calculated on two data sets, one that included humans and one that consisted only of nonhuman primates.

The validity of the Frankfurt plane was evaluated by determining 1) whether it showed unusually high variability as measured by its standard deviation, 2) whether human and nonhuman primates exhibited similar values, as evaluated by examination of a histogram of values for all primates studied, and 3) whether the relative orientations of the Frankfurt and orbital planes indicate that the former might have been held horizontally in fossil hominids.

RESULTS

It is worth reiterating that the three primary kinematic measurements are angles taken relative to gravity, but they are not read in the same manner. The Frankfurt plane is horizontal when it is oriented at 90°, and it slopes anteriorly and inferiorly when inclined at less than 90°. The orbital plane is vertical when it is oriented at 0°, and the orbits face anteriorly and inferiorly as the angle increases in value. Negative values indicate that the species looks somewhat superiorly. The neck is horizontal when it is oriented at 90° and becomes more vertically inclined as the angle approaches 0°.

Head posture

The head posture data presented in Table 1 are summarized in Figure 3, which shows the distribution of species means for orbit inclination and the inclination of the Frankfurt plane. For the purposes of this figure, head posture values for species that engaged in two modes of locomotion were calculated as the average of the mean for each locomotor mode. Regarding orbit inclination, the species clustered into a tight, peaked distribution whose mean is 13.7°. In other words, most primate species hold their heads such that their orbits face anteriorly and slightly inferiorly, as indicated by the fact that the values for these species are at or slightly above zero. *Symphalangus syndactylus* is the only species that looks superiorly at the

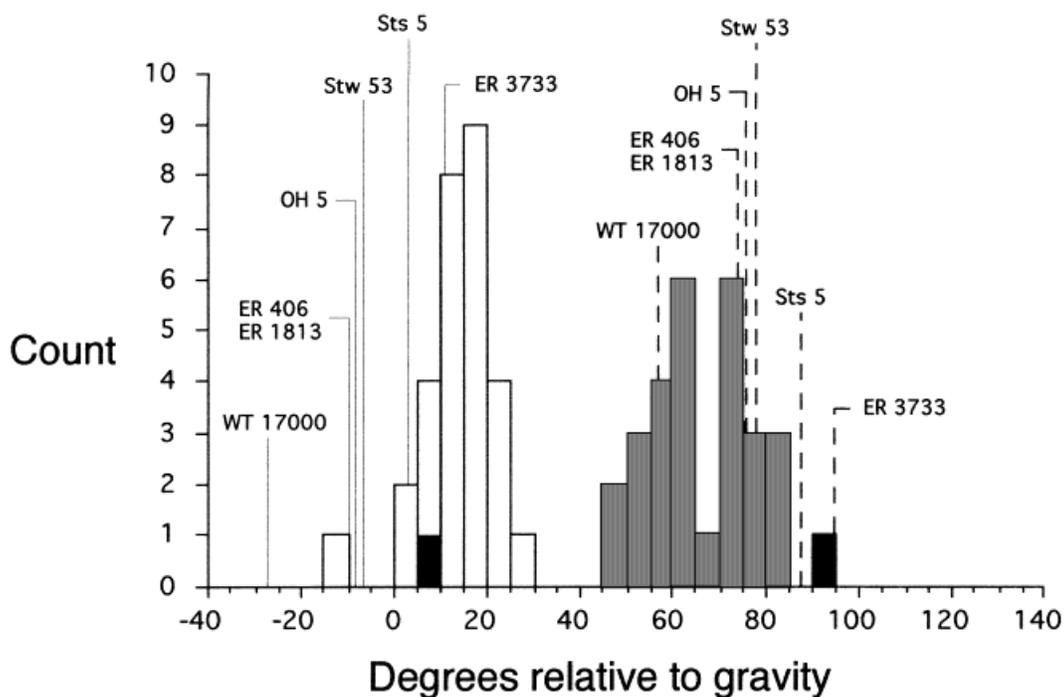


Fig. 3. Histogram of the distribution of species means for head-posture measurements. White vertical bars indicate species means for orbit inclination. Grey vertical bars indicate species means for the inclination of the Frankfurt plane. Black vertical bars indicate the values of *Homo sapiens* for the two measurements. An orbit inclination of 0° indicates that the orbits are vertical.

The Frankfurt plane is horizontal when inclined at 90°. Solid vertical lines indicate the orbit inclination of fossil hominid specimens, assuming that the Frankfurt plane is oriented as in humans. Dashed vertical lines indicate the inclination of the Frankfurt plane in hominids, assuming that the orbital plane is oriented as in humans.

time our head orientation measures were taken.

The data on the Frankfurt plane indicate that, in most primates, this plane is not held horizontally during locomotion but is inclined such that infraorbitale is inferior to porion. Moreover, humans are outliers to the rest of primates, being the only species in which the plane is held horizontally.

The standard deviations of mean orbit inclination and mean Frankfurt plane inclination are 8.0 and 11.2, respectively. This is consistent with the observation (Fig. 3) that the Frankfurt plane distribution is flatter than the distribution of orbital plane values and appears bimodal. Note that the coefficient of variation (CV) was not employed as a measure of variability because the mean of an angle (and thus its CV) varies according to its frame of reference. For instance, an angle of 160° is logically equivalent to one of 20°, but the means are very different.

TABLE 2. Angular difference between the orbital and Frankfurt planes in fossil hominids

Specimen	Difference (in degrees)
Sts 5	96.4
KNM-WT 17000	66.2
OH 5	85.6
KNM-ER 406	83.7
KNM-ER 1813	83.7
Stw 53	87.2
KNM-ER 3733	104.1

Head posture in early hominids cannot be directly observed, but it is possible to measure the angulation between the Frankfurt and orbital planes on fossil crania (Table 2). If it is assumed that all fossil hominids held their heads such that the orientation of the Frankfurt plane was the same as in humans, then many fossil hominids would have held their orbits such that they faced superiorly (Fig. 3). In contrast, if it is assumed that early hominids had a human-

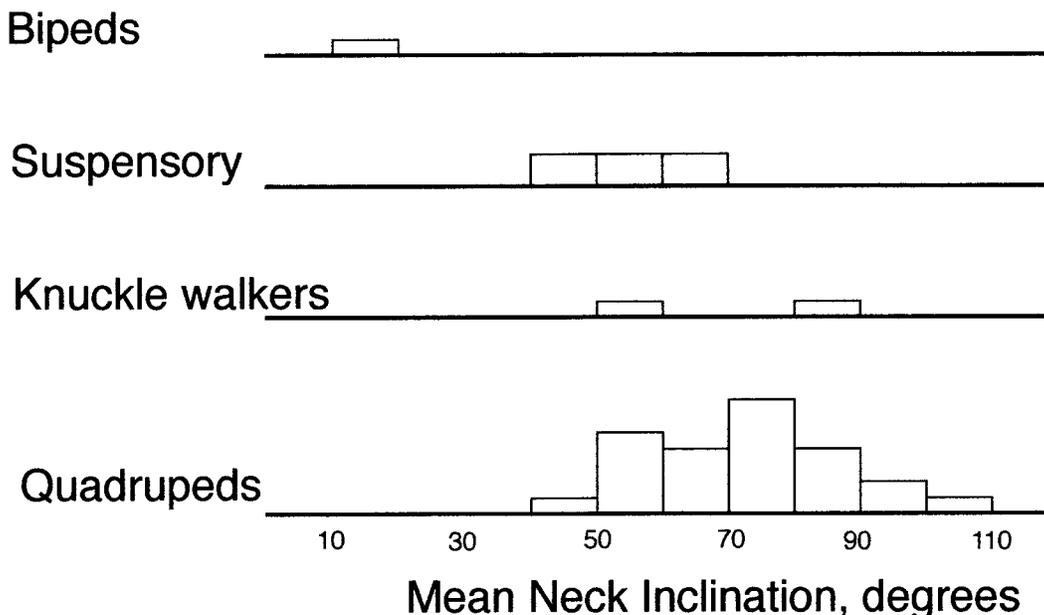


Fig. 4. Histograms of mean neck inclination in primates divided according to locomotor mode.

like value for orbit inclination, then the orientation of the Frankfurt plane falls easily within the range of living primates (Fig. 3).

Neck posture

It is obvious from Table 1 that quantitative kinematic data on neck inclination represent a vast improvement over qualitative generalizations such as pronograde and orthograde (Fig. 4). For instance, it would be misleading to characterize brachiators as having orthograde neck posture because necks in these species are actually fairly strongly inclined. Moreover, although quadrupeds are the only species to exhibit horizontally inclined necks, the range of neck inclination in quadrupedal species (48.5–107.6°) almost encompasses that of the brachiating species (47.0–63.1°). The best example of the inadequacy of using locomotor mode as a surrogate for neck posture is provided by the African apes. Given that *Pan* and *Gorilla* both employ a unique form of locomotion (knuckle-walking), one would expect them to have similar values for neck inclination. In fact, these species differ on average by about 25°.

This is not to say that neck inclination is unaffected by locomotor mode. For instance, *t*-tests revealed that within *L. lagotricha* and *A. fusciceps* brachiation was associated with significantly more vertical neck posture than quadrupedalism ($P < .0001$). The same relationship was nearly significant in *A. geoffroyi* ($P = .057$), but the comparison was hindered by small sample size. Within *C. guereza*, neck posture was significantly more horizontal during leaping than during quadrupedal walking ($P < .0001$). Of course, intraspecific comparisons may not be directly comparable to interspecific ones; selection does not act to transform the cranial morphology of a spider monkey as it switches from brachiation to quadrupedalism. Thus, although intraspecific comparisons reveal that neck inclination is influenced by locomotor mode, interspecific comparisons indicate that this influence is not so strong as to support broad, qualitative generalizations.

Correlations

Pearson correlation coefficients for bivariate comparisons of CBA, AOA, IRE, and the HNA are shown in Table 3. All four variables are significantly correlated with each other

TABLE 3. Bivariate correlations between flexion, orbital kyphosis, relative brain size and posture

	CBA	AOA	IRE	HNA
Correlations among all species				
CBA	1.00			
AOA	.74*	1.00		
IRE	-.83*	-.71*	1.00	
HNA	.76*	.81*	-.71*	1.00
Correlations among nonhuman primates				
CBA	1.00			
AOA	.54*	1.00		
IRE	-.68*	-.38	1.00	
HNA	.65*	.73*	-.60*	1.00

* $P < .05$.

in the all-species sample, as they are in the nonhuman primates sample, with the exception of AOA and IRE. Bivariate plots of HNA against the other three variables are shown in Figure 5, and these reiterate the degree to which humans are outliers. Similar plots between CBA, AOA, and IRE are presented in Ross and Ravosa (1993) and Ross and Henneberg (1995).

Partial correlation coefficients are shown in Table 4. In both samples, when variation in other variables is accounted for, basicranial flexion (CBA) is found to be significantly correlated with relative brain size (IRE), and the head-neck angle (HNA) is found to be correlated with orbital frontation (estimated by AOA). Relative brain size and posture are not significantly related to each other when AOA and CBA are taken into account.

DISCUSSION

A number of unavoidable factors may have affected the kinematic data. First, due to a dearth of subjects or because dominant individuals in a group monopolized the food rewards, there were usually only one or a few individuals filmed per species. Thus, interindividual variation is not well documented by our data set. Second, the substrates varied according to the conditions under which the subjects were filmed (Table 1). Substrates may have an important effect on head posture because an irregular or arboreal substrate might encourage a primate to focus attention on it. Terrestrial substrates included the ground and the floor of a cage. A cage floor contains gaps, and thus is perhaps a somewhat more irregular

substrate than the ground. Arboreal substrates were all horizontal and included iron bars, wooden branches, and wooden beams of varying diameters. When possible, subjects were filmed on substrates that matched their habitual mode of locomotion (i.e., arboreal quadrupeds on arboreal substrates), but this could not be achieved for every species. Inclined substrates tended not to be available. Future work should determine whether substrate inclination has a strong effect on head and neck posture. Third, posture (particularly head posture) could have been influenced by the fact that under controlled and semicontrolled conditions primates were coaxed to move in front of the cameras with food rewards. Qualitatively, such a bias did not appear to be common; most often, subjects saw the food reward but then adjusted their head posture during locomotion so they were not looking directly at it. Finally, the neck posture measurement may be unduly influenced by the soft tissue structures of the neck, particularly the nuchal muscles. Refshauge et al. (1994) found that the mean inclinations of the dorsal surface of the neck and the cervical vertebrae differed by only 4° in a sample of humans, but this discrepancy is likely to be greater in species with greater nuchal muscle mass, such as *G. gorilla*.

For these reasons and because most species were filmed under semicontrolled conditions, the data presented here should be considered approximate. Nonetheless, these data are still considerably more accurate than the qualitative characterizations (pronograde or orthograde) employed by Ross and Ravosa (1993).

Head posture

Most primate species were found to hold their heads with their orbits facing anteriorly and slightly inferiorly. The exception to this generalization is *Symphalangus syndactylus*, which looked superiorly at the time our head posture measures were taken. This occurred because siamangs must look up during brachiation to locate their next handhold. In fact, all brachiators change their head posture throughout the swing cycle, so at the beginning of the cycle the orbits face slightly inferiorly and at the end of the cycle

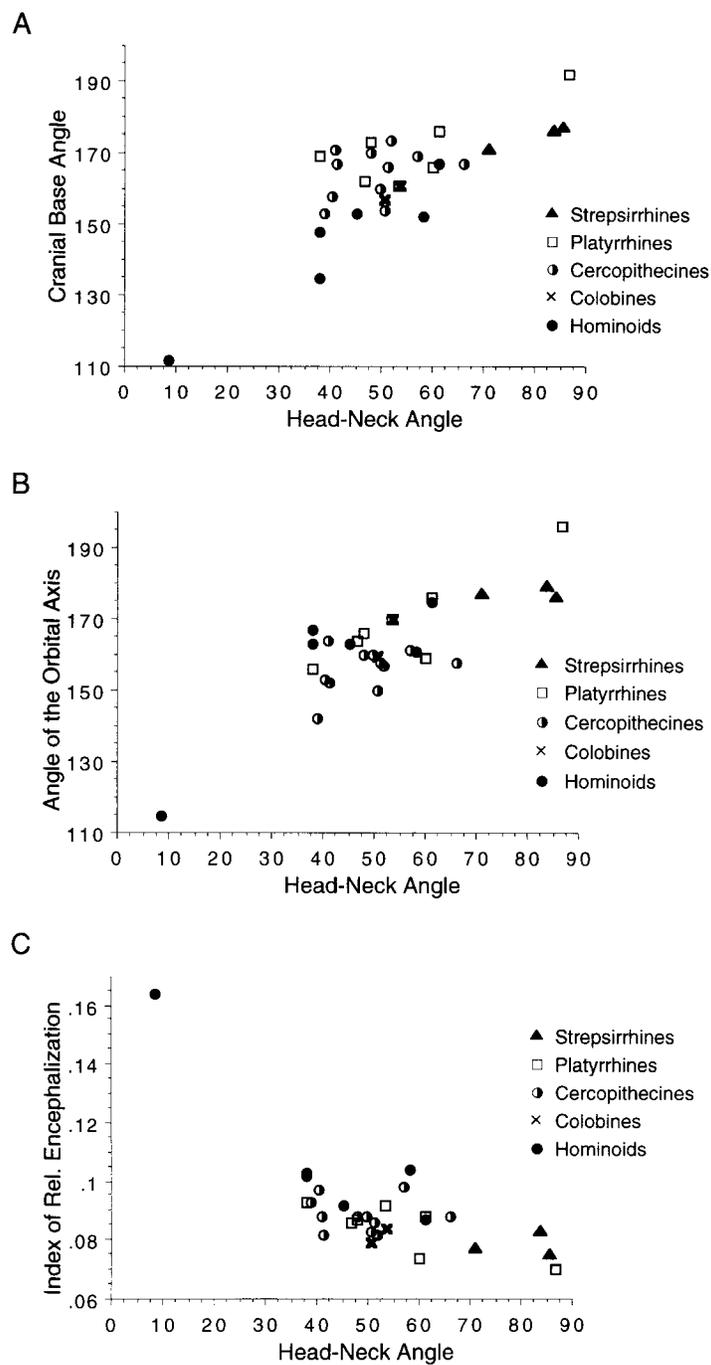


Fig. 5. Bivariate scatterplots of HNA vs. CBA (A), AOA (B), and IRE (C).

they face somewhat superiorly. At approximately midswing (when orbit inclination was measured), all species raise their heads. The value for orbit inclination in *S. syndactylus*

is exceptional compared to other brachiaturs because this species tended to raise its head earlier in the swing cycle (just before midswing rather than at or after midswing).

TABLE 4. Partial correlations between flexion, orbital kyphosis, relative brain size and posture

	CBA	AOA	IRE	HNA
Partial correlations among all species				
CBA	1.00			
AOA	.15	1.00		
IRE	-.59*	-.17	1.00	
HNA	.29	.55*	-.08	1.00
Partial correlations among nonhuman primates				
CBA	1.00			
AOA	.19	1.00		
IRE	-.49*	-.18	1.00	
HNA	.21	.61*	-.33	1.00

* $P < .05$.

Because head posture changes during the locomotor cycle in these species, the measurements recorded here represent gross simplifications of the actual head postures employed by them. Consequently, the postural data for these species must be viewed cautiously. In most other species, head posture remained qualitatively consistent throughout a cycle, but clearly a quantitative study of intracycle variability in head posture is warranted.

In general, however, orbit inclination data confirmed the notion that primates maintain an anteriorly directed visual field. In reality, the visual field faced somewhat inferiorly, consistent with the fact that most primate species utilize an inferiorly placed substrate. Accordingly, the premise of the postural hypothesis was supported.

The observation that all primates maintain an anteriorly directed visual field raises the possibility that the orbital plane may be more suitable than the Frankfurt plane for use as a registration plane in craniometric studies aimed at studying morphological correlates of posture. Although the orbit inclination measure shows lower variability than the Frankfurt plane, we do not feel that this difference alone precludes the Frankfurt plane from use as a registration plane. However, when one examines the values for human and nonhuman primates, a different picture is found: humans are well within the primate range for orbit inclination, but they are outside the range of nonhuman primates for Frankfurt plane orientation (Fig. 3). Humans are the only species in which the Frankfurt plane is truly horizontal; the plane is inclined in every other primate species, and in some cases the inclination is quite steep.

This result has implications for functional craniometric studies, as can be demonstrated by considering the foramen magnum. There has been considerable interest in how the foramen magnum is oriented and positioned during habitual postures in human and nonhuman primates (e.g., Dart, 1925; Senyurek, 1938; Schultz, 1942, 1955; DuBrul, 1950; Ashton and Zuckerman, 1951, 1952, 1956; Le Gros Clark, 1955; DuBrul and Laskin, 1961; Moore et al. 1973; Adams and Moore, 1975; Demes, 1985, 1986; Luboga and Wood, 1990). If one measures the orientation of the foramen relative to Frankfurt Horizontal, as most of the above studies have done, then the data for human and nonhuman primates will not be comparable because the orientation of Frankfurt Horizontal itself differs between humans and other species. In contrast, humans and nonhuman primates have similar values for orbit inclination during locomotion, suggesting that studies attempting to determine the influence of posture on the orientation and position of the foramen magnum should instead use the orbital plane, rather than the Frankfurt Horizontal.

Further evidence on the utility of the orbital plane (and the inapplicability of the Frankfurt plane) comes from a consideration of head posture in fossil hominids. As noted, when certain specimens are oriented in Frankfurt Horizontal, then they are positioned such that their orbits face superiorly (Fig. 3). Such an orientation differs from that of all but one extant primate species and is unreasonable given that bipedal hominids have an inferiorly placed substrate (i.e., the ground). However, when hominid crania are oriented such that their orbits are inclined as in humans, then their Frankfurt planes are inclined as in other primates. In summary, the orbital plane seems much more likely than the Frankfurt plane to reflect habitual head posture across a broad sample of primates and early hominids. It should be noted, however, that in *H. ergaster* and presumably later hominids the Frankfurt plane was probably inclined to a degree similar to that seen in modern humans. Thus, the Frankfurt plane may be suitable for use in some studies concerning the later aspects of human evolution.

It should be noted, of course, that other planes of head posture have been applied to the study of human and primate evolution. In particular, several studies (e.g., Delattre and Fenart, 1960, 1963) have used the vestibular plane under the assumption that the lateral semicircular canals are oriented horizontally in primates and other vertebrates (Girard, 1911, 1923). This is a common assumption that has yet to be functionally explained and for which there is little empirical support. The semicircular canals do not orient the head in space, this being the job of the otolith organs, the saccule and the utricle (Kandel et al., 1991; Graf et al., 1995a). The semicircular canals are instead used to register angular acceleration in three dimensions. In order to accomplish this, the canals must be oriented perpendicular to each other, but there is no obvious reason any of the canals needs to have a particular orientation relative to gravity. It is therefore not surprising that recent studies have found that the canals are inclined during resting postures and locomotion in some mammals (Vidal et al., 1986; Graf et al., 1995a,b), although there is some evidence that the canals may be brought into earth-horizontal during "alert" postures (Graf et al., 1995b).

Nevertheless, the semicircular canals do play a role in postural control and coordination of body movements as well as coordinating eye and head movements through their neuronal connections to the extraocular motor system (e.g., Kandel et al., 1991; Graf et al., 1995a,b). Moreover, although they are not oriented horizontally, the lateral semicircular canals do display a relatively limited range of orientations relative to gravity in resting postures. Our data on orbital plane orientation suggests a possible explanation for this regularity. Functional links between the lateral semicircular canals and the medial and lateral rectus muscles mediate the horizontal vestibulo-ocular reflex, whereby each lateral semicircular canal excites contractions in its ipsilateral medial rectus and contralateral lateral rectus muscles. This reflex ensures that head movements which stimulate the lateral canals are accompanied by compensatory movements of the eye, facilitating fixation of objects during relative movements of the observer. The phyloge-

netically conservative nature of this functional system may mean that the lateral semicircular canals and the medial and lateral rectus muscles are maintained in roughly the same plane in different species. Consequently, when the extraocular muscles are oriented horizontally, so will be the lateral semicircular canals. It seems reasonable to hypothesize that the medial and lateral rectus muscles are oriented approximately perpendicular to the orbital plane measured here, suggesting that they and the lateral semicircular canals have a relatively constant orientation vs. the gravity vector purely because of the relatively constant orientation of the orbital margin.

A full evaluation of the vestibular plane and its applicability to paleoanthropology as a registration plane would require knowledge of how this plane is oriented during locomotion in a variety of primate species (de Beer, 1947; Bull, 1969). Head posture data collected in the present study should facilitate such an evaluation; if the inclination of the vestibular plane relative to the Frankfurt or orbital planes is collected in the species examined here, then the postural data presented above will allow the calculation of the orientation of the vestibular plane relative to the gravity vector during locomotor activities.

Determinants of flexion

Bivariate comparisons reveal all four variables examined here (CBA, AOA, IRE, HNA) to be significantly correlated with each other. However, partial correlation analyses provide a more subtle picture of the patterns of correlation between these variables. When the variability in relative brain size (IRE) is taken into account, neither posture (HNA) nor orbital kyphosis (AOA) retains a significant correlation with flexion (CBA). It would appear that the correlations between flexion and both HNA and AOA in the bivariate comparisons are being mediated by correlations between these variables and IRE. This suggests that relative brain size is the most important determinant of the degree of basicranial flexion, whereas habitual head and neck posture has no significant effect on flexion. This result confirms the results obtained by Ross and Ravosa (1993) using

more simplistic, qualitative descriptions of posture.

Similarly, when head and neck posture is taken into account, neither CBA nor IRE is found to be significantly correlated with AOA. Rather, when other variables are controlled for, variation in the degree of orbital kyphosis (AOA) is significantly correlated only with relative head and neck posture (HNA). A factor that may contribute to this correlation is the fact that the orbital axis (used to calculate AOA) is probably roughly perpendicular to the orbital plane (used to calculate HNA) in most species. Thus, the orientations of the axis and plane might be expected to covary, with the consequence that HNA and AOA would covary as well.

Ross and Ravosa (1993) found significant partial correlations between CBA and both AOA and IRE across primates and haplorhines and among colobines. Among platyrrhines, AOA was found to be more important than IRE in determining CBA. Ross and Ravosa's (1993) results are clarified by the present study: that is, among the animals examined here—predominantly catarrhines—flexion is predominantly determined by relative brain size and AOA is determined primarily by head and neck posture.

This latter finding corroborates a suggestion advanced elsewhere (Dabelow, 1929; Ross, 1995) that high degrees of orbital kyphosis (i.e., orbital margins that are "rotated" inferiorly relative to the rest of the skull) might be expected in orthograde animals as one means of reorienting the visual field. This explanation was invoked to explain the high degrees of orbital frontation in indriids and callitrichids. The present study is consistent with the hypothesis that orthograde animals manifest vertically oriented orbital margins (equivalent to a ventrally deflected orbital axis and low value for AOA) even when the degree of basicranial flexion and relative brain size are taken into account.

These results suggest that although the relative size of the brain can mediate the orientation of the upper face via basicranial flexion, habitual head and neck posture have an additional effect independent of flexion.

Implications for hominid evolution

Ross and Henneberg (1995) suggested that although basicranial flexion in anthropoid primates is primarily determined by relative brain size (Ross and Ravosa, 1993), the hominid basicranium reached its maximal degree of flexion early in hominid evolution, possibly in *Australopithecus africanus*. This maximal limit exists because the basicranium cannot flex to such an extent as to be in danger of occluding the respiratory airway. Subsequent to this stage of basicranial evolution, further increases in relative brain size must be accommodated by other means.

The present study confirms the importance of relative brain size in determining the degree of basicranial flexion among primates and suggests that head and neck posture has little influence on the degree of flexion among primates. However, it does suggest that head and neck posture influences orbital axis orientation. This may explain why anatomically modern humans and the Kabwe skull exhibit orbital axes that are more ventrally deflected than expected for their degree of basicranial flexion (Ross and Henneberg, 1995). Rather than being a mechanism for accommodating a hypertrophied brain in the context of constraints on basicranial flexion (Ross and Henneberg, 1995), a ventrally deflected orbital axis in humans may function instead to bring the eyes and orbits into the correct, anterior orientation.

Regarding head posture, the data indicate that the orbital plane may approximate a natural plane of head posture insofar as the orbital plane exhibits a fairly consistent relationship with gravity across diverse primates. The competing plane, Frankfurt Horizontal, is truly horizontal only in humans and in all likelihood *H. ergaster* and later hominids. Thus, the use of Frankfurt Horizontal as a registration plane still seems justified in certain studies restricted to the later half of human evolution (e.g., comparisons between archaic and anatomically modern humans). However, the Frankfurt plane seems unsuited for studies that concern early hominid evolution. This certainly is true if the measurements being taken have a functional relationship with posture or

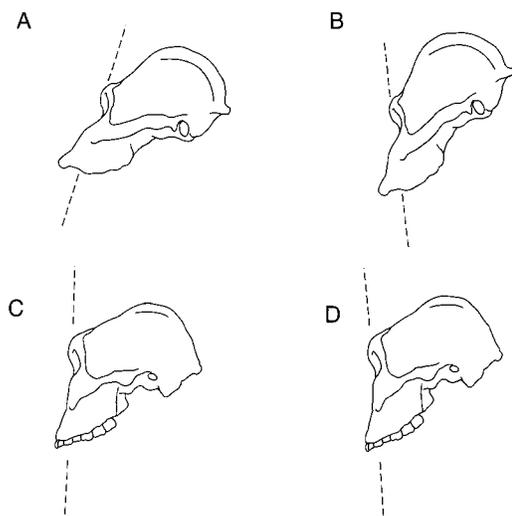


Fig. 6. Head posture and interpretations of early hominid cranial morphology. **A:** KNM-WT 17000 oriented in Frankfurt Horizontal. **B:** KNM-WT 17000 oriented such that the orbital plane faces slightly inferiorly. **C:** OH 5 oriented in Frankfurt Horizontal. **D:** OH 5 oriented such that the orbital plane faces slightly inferiorly.

otherwise are meant to reflect the configuration of a structure relative to the position of the head as it is held in habitual postures. For such studies, the orbital plane provides a much more suitable registration plane.

Even in a nonfunctional context, an acceptance of the orbital plane as a registration plane has implications for how early hominid cranial morphology is interpreted. For instance, Figure 6 depicts two fossil crania, KNM-WT 17000 and OH 5, oriented in Frankfurt Horizontal (Fig. 6A,C) and in such a way as to make the orbits face slightly inferiorly (Fig. 6B,D). In the Frankfurt plane, which is the standard view (e.g., Tobias, 1967; Walker et al., 1986; Walker and Leakey, 1988), it seems obvious that the two crania differ in facial orientation and prognathism but are generally similar in terms of facial hafting (i.e., the relationship between the top of the face and the frontal squama). However, when the skulls are oriented in a plane that is more likely to represent habitual head posture, the differences in facial prognathism and orientation seem less pronounced, whereas there is a dramatic difference in how the neurocranium

attaches to the face. Obviously, there is no clear functional reason why characters such as these should be related to head posture, so the justification for choosing the orbital plane over the Frankfurt plane is not as strong as it would be if a functional relationship with posture existed. It is clear, however, that without a reference to head posture the Frankfurt plane is merely arbitrary, and it could be argued that data collected against this plane are arbitrary as well. Certainly it is disturbing that something as innocuous as how one holds a cranium can have a substantial effect on how one characterizes that cranium, and it is a factor that needs to be considered more critically in studies of early human evolution.

CONCLUSIONS

Attempts to relate comparative cranial morphology to posture within primates have been limited by an absence of quantitative kinematic data on head and neck posture. With respect to basicranial flexion, data presented here indicate that although the premise of the postural hypothesis was confirmed (that primates maintain an anteriorly directed visual field), head and neck posture is not the primary determinant of flexion. Rather, flexion is influenced principally by relative brain size, a result that is consistent with prior studies.

In a broader biological context, the kinematic data are relevant to any functional study examining the relationship between cranial morphology and posture not only because information about head and neck posture may be necessary to test those hypotheses but also because the head posture data suggest that the orbital plane may be suitable for use as a registration plane for collecting craniometric measurements.

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