Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion

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THE upright posture and obligatory bipedalism of modern humans are unique among living primates. The evolutionary history of this behaviour has traditionally been pursued by functional analysis of the postcranial skeleton and the preserved footprint trails of fossil hominids. Here we report a systematic attempt to reconstruct the locomotor behaviour of early hominids by looking at a major component of the mechanism for the unconscious perception of movement, namely by examining the vestibular system of living primates and early hominids. High-resolution computed tomography was used to generate cross-sectional images of the bony labyrinth. Among the fossil hominids the earliest species to demonstrate the modern human morphology is *Homo erectus*. In contrast, the semicircular canal dimensions in crania from southern Africa attributed to *Australopithecus* and *Paranthropus* resemble those of the extant great apes. Among early *Homo* specimens, the canal dimensions of Stw 53 are unlike those seen in any of the hominids or great apes, whereas those of SK 847 are modern-human-like.

Functional analyses of hominid postcranial fossils and preserved footprint trails have prompted conflicting interpretations, characterizing the early stages of hominid locomotion either as a modern human-like obligatory bipedalism[1,2] or as a more primitive behaviour which combined arboreal climbing with a bipedal gait unlike that seen in modern humans[3,4]. We have explored the potential of a new approach to the study of early hominid locomotion by focusing on the vestibular apparatus, part of the system of receptors which monitors movements. Modern human locomotor behaviour makes particular demands on the vestibular apparatus for it involves the maintenance of an upright body posture by balancing on very small areas of support. The morphology of the vestibular apparatus that is preserved in fossils comprises the three bony semicircular canals, and their

dimensions reflect the arc size of the enclosed membranous semi-circular ducts. Theoretical and experimental neurophysiological evidence indicates a direct relationship between duct size and the sensitivity and time constants of the semicircular canal monitoring system[5-9], and studies of birds and prosimians have suggested that canal size and locomotor behaviour are interrelated[10-12].

Methods for visualization of the bony labyrinth in fossil hominid crania using high-resolution computed tomography (CT) have been reported[13,14]. The sample, comprising 31 extant primate species and 12 hominid fossils, is listed in Table 1. Height and width measurements of the arc of each semicircular canal were taken from CT scans, and these were used to calculate the radius of curvature (R) of the arc (Fig. 1), which is given in Table 2 for the great ape and hominid species.

In the extant primate sample, the arc size of each of the three semicircular canals is correlated with body mass (Fig. 2). Taking body mass into account, modern humans have larger anterior
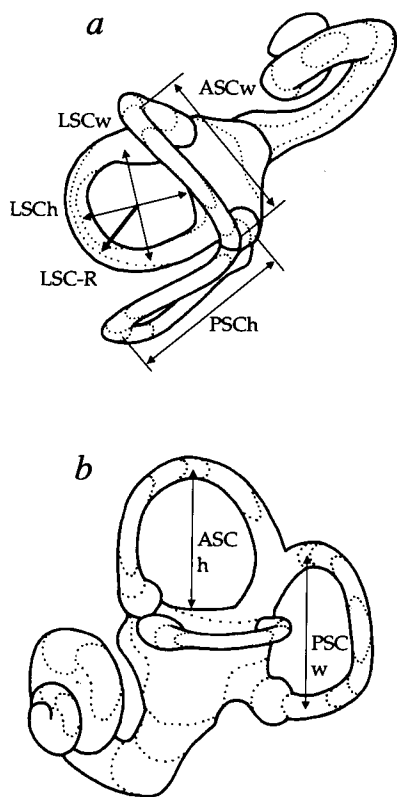

FIG. 1 The superior (a) and lateral (b) aspects of a left human bony labyrinth, reconstructed from transverse and sagittal CT scans of the temporal bone region respectively. Labyrinth outlines that appear in individual scans are shown as dotted lines. The method used to obtain these CT scans is described elsewhere[13,14,30]. The height (h) and width (w) of the anterior (ASC), posterior (PSC) and lateral (LSC) semicircular canals were taken, using landmarks on the wall of the vestibule and in the centre of the canals' lumina (ASCw, PSCh, LSCh and LSCw in transverse CT scans, and ASCh and PSCw in sagittal scans). Experimentally, these dimensions can be taken from CT scans with a maximum error of ±0.1 mm[30]. The radius of curvature (R) of each canal, listed in Table 2 and plotted in Fig. 2, is defined as half the average of the canal height and width ($0.5(h+w)/2$), and is indicated for the lateral canal here (LSC-R). The membranous semicircular ducts seem to be consistently located along the outer wall of the bony canals[31,34,35], and dimensions defined using landmarks on the outer canal wall may therefore give better estimates of the functionally important duct sizes. Such landmarks were not employed here, however, as they result in less accurate measurements than landmarks in the centre of the canal's lumen when taken from CT scans[30].

TABLE 1 Number of specimens for the extant species

	CT	Published	Code
Extant species			
Homo sapiens	53	20 (ref. 31)	Hs
Pan troglodytes	7	1 (ref. 32)	Pt
Pan paniscus	6	—	Pp
Gorilla gorilla	6	1 (ref. 32)	Gg
Pongo pygmaeus	7	1 (ref. 32)	Po
Hylobates symphalangus	2	—	
Hylobates moloch	1	—	
Hylobates pileatus	1	—	
Macaca fascicularis	3	—	
Macaca mulatta	—	15 (ref. 33)	
Macaca nemestrina	—	1 (ref. 32)	
Nasalis larvatus	1	—	
Cercopithecus aethiops	—	1 (ref. 34)	
Cercopithecus nictitans	—	1 (ref. 34)	
Papio cynocephalus	—	1 (ref. 34)	
Papio hamadryas	—	1 (ref. 32)	
Papio ursinus	1	—	
Theropithecus gelada	1	—	
Mandrillus sphinx	1	—	
Lagothrix lagothricha	1	—	
Alouatta seniculus	1	1 (ref. 32)	
Saimiri sciureus	1	17 (refs 33, 35)	
Cebus sp.	—	1 (ref. 35)	
Aotus trivirgatus	—	1 (ref. 35)	
Callithrix jacchus	—	1 (ref.34)	
Tarsius bancanus	—	1 (ref. 12)	
Lemur macaco	—	1 (ref. 32)	
Lemur mongoz	—	1 (ref. 34)	
Nycticebus coucang	—	2 (refs 12, 34)	
Propithecus diadema	1	—	
Indri indri	1	—	
Fossil hominids			
Homo erectus	OH9, Sangiran 2, Sangiran 4		He
Early *Homo*	Stw 53g (d), SK 847		53 —
Australopithecus africanus	Taung, Sts 5, Sts 19, MLD 37/38		Aa
Paranthropus robustus	SK 46, SK 47, SK 879		Pr

Measurements were taken from CT scans and from the literature. Where both sources provide canal dimensions for the same species, these correspond well[30]. For the great ape and hominid species, the codes used in Fig. 2 are given.

and posterior canals and a smaller lateral canal than the great apes (Fig. 2). These differences are also clearly demonstrated by the relative canal sizes listed in Table 2. Among the fossil hominids, the australopithecines show great-ape-like proportions and *H. erectus* shows modern-human-like proportions. The specimen Stw 53, provisionally attributed to *H. habilis*, differs from all other hominids by having a particularly large lateral semicircular canal, and this morphology shows greatest similarity to the pattern observed for large cercopithecoids. These unexpected canal proportions were noted for the perfectly preserved, air-filled, left labyrinth in Stw 53g. The right petrous pyramid of the same individual, Stw 53d, is internally fragmented and the only two measurements (ASCw, PSCw) that could be taken are identical to those on the left side. The specimen SK 847 has not been included in Fig. 2 because no realistic body mass estimates are yet available. However, its absolute and relative canal dimensions show closest resemblance to modern humans (Table 2). It is worth mentioning that the planar orientations of the semicircular canals in the cranium (the anterior and posterior ones relative to the midsagittal plane, and the lateral one relative to the basicranial orientation basion–nasion) are not significantly different in modern humans, the African great apes and the fossil hominids.

TABLE 2 Absolute and relative radii of curvatures of the anterior, posterior and lateral semicircular canals of the great apes and hominids

| | Absolute radius of curvature | | | | | | Relative radius of curvature | | |
| | ASC-R | | PSC-R | | LSC-R | | ASC | PSC | LSC |
	Mean	s.d.	Mean	s.d.	Mean	s.d.			
Homo sapiens	3.2	0.24	3.1	0.31	2.3	0.44	37	36	26
Pan troglodytes	2.7	0.20	2.8	0.25	2.5	0.25	34	35	31
Pan paniscus	2.6	0.19	2.5	0.16	2.4	0.18	35	34	32
Gorilla gorilla	2.9	0.15	3.0	0.28	3.0	0.25	32	34	34
Pongo pygmaeus	2.7	0.25	2.5	0.21	2.4	0.11	35	33	31
Homo erectus	3.2	0.06	3.1	0.25	2.1	0.23	38	37	25
SK 847	3.1	—	2.9	—	2.3	—	37	35	28
Stw 53g	2.9	—	2.8	—	2.8	—	34	33	33
Australopithecus africanus	2.4	0.26	2.6	0.19	2.2	0.17	34	36	30
Paranthropus robustus	2.6	0.12	2.7	0.26	2.5	0.12	34	34	32

The absolute radius is given in millimeters (mean and standard deviation listed for species), and the relative radius in per cent (sum of the three canals is 100%). ASC, PSC and LSC represent anterior, posterior and lateral semicircular canals, respectively.

As all four great ape species have similarly proportioned semi-circular canals, it seems likely that this pattern represents the ancestral condition of the hominids. This is supported by the fact that the oldest fossil hominids thus far investigated show the great-ape condition. Hence, the evolutionary history of the human labyrinth is characterized by the subsequent enlargement of the anterior and posterior semicircular canals and reduction of the lateral canal. The exact functional consequences of enlarging the arc of a semicircular duct and canal are not fully understood, because of uncertainty over some fundamental aspects, such as the nature of cupula movement in the ampulla[15]. How-

ever, models of endolymph movement as well as the results of neurophysiological experiments indicate a link between a larger arc size and an increase in sensitivity[5-9]. Increased sensitivity of the vertically oriented anterior and posterior canals in humans would make sense because the role of the vestibular system in coordinating upright bipedal behaviour through the vestibular reflexes particularly involves monitoring body movements in the vertical plane.

Among the fossil hominids investigated, the earliest species to demonstrate the modern human semicircular canal morphology is *Homo erectus*. Hence, if the enlargement of the anterior and
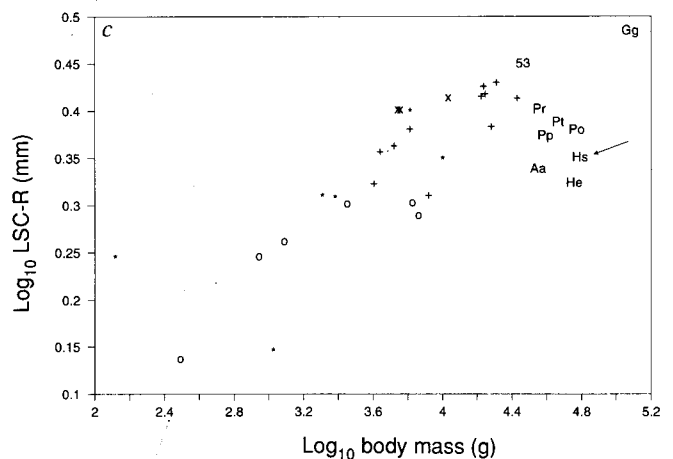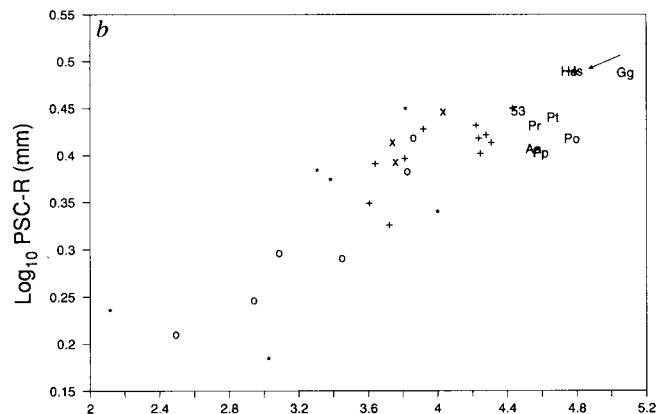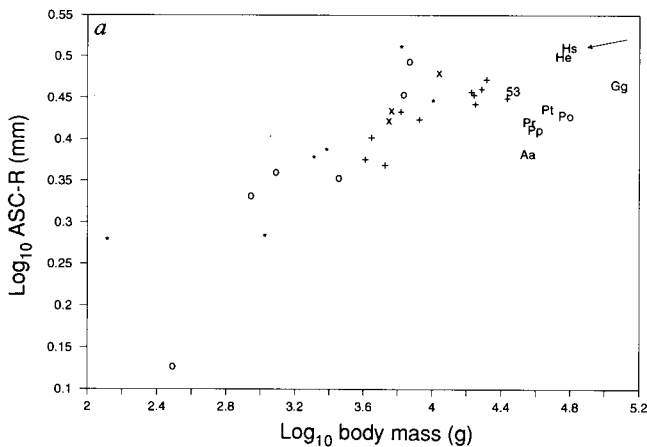

FIG. 2 Bivariate double logarithmic plots between the estimated body mass and the average radii of curvature of *a*, the anterior; *b*, the posterior, and *c*, the lateral semicircular canal (ASC-R, PSC-R, LSC-R). Correlation coefficient *r* for the extant species 0.782, 0.850 and 0.796 respectively. The legend for the great ape and hominid species is given in Table 1; ×, hylobatids; +, cercopithecoids, ○, ceboids; *, prosimians. Arrow indicates the position *Homo sapiens*; in *b*, the labels of *H. sapiens* and *H. erectus* and those of *Australopithecus africanus* and *Pan paniscus* overlap. Body masses of the extant species were taken from ref. 36, body mass estimates of the australopithecines, Stw 53 ('small morph' of *H. habilis*) and *Homo erectus* were taken from refs 17 and 37.

posterior canals is functionally related to modern human-like obligatory bipedalism, then at least in this respect the vestibular apparatus of the australopithecines was not adapted to this type of locomotor behaviour. These observations support studies of the postcranial fossil record which have concluded that *H. erectus* was an obligatory biped[16,17], whereas *A. africanus* showed a locomotor repertoire comprising facultative bipedalism as well as arboreal climing[18-20]. The labyrinthine evidence is consistent with proposals that bipedalism in australopithecines was characterized by a substantial postural component[21,22], and by the absence of more complex movements such as running and jumping[3]. Such behaviour will predominantly make functional demands on the utricular and saccular part of the vestibular apparatus, and is therefore not clearly reflected in the semicircular canal morphology. It is not evident from the semicircular canal proportions that *P. robustus* had a less arboreal locomotor repertoire than *A. africanus*, as has been concluded from their postcranial morphology[23].

The specimen Stw 53, provisionally referred to *H. habilis*, has semicircular canal proportions not seen in any of the other fossil or extant hominids or great apes. Functional interpretation of this morphology can only be speculative, but the similarity with the canal proportions in large cercopithecoids suggests that Stw 53 relied less on bipedal behaviour than the australopithecines. Interestingly, similar observations were reached from an analysis of the postcranial bones of OH 62 (ref. 4), a specimen that has been assigned to the same species as Stw 53 on the basis of similarities in their maxillary and dental morphology[24]. Phylogenetically, the unique labyrinth of Stw 53 represents an unlikely intermediate between the morphologies seen in the australopithecines and *H. erectus*.

The specimen SK 847 has both been associated with *H. erectus*[25,26] and *H. habilis*, in particular with Stw 53 (ref. 27). The modern-human-like labyrinth of SK 847 is consistent with the attribution to *H. erectus*, and the extreme differences in labyrinthine morphology between SK 847 and Stw 53 make attribution of both specimens to the same species, on this evidence alone, highly unlikely. The specimen Sts 19 is part of the conventional *A. africanus* hypodigm, but has also been considered as a basicranium of early *Homo*[28]. As the labyrinth of Sts 19 is very similar to that in the other three *A. africanus* specimens, and major aspects of its overall morphology, such as petrous pyramid orientation and basicranial flexion, can easily be accommodated in normal species variation[29,30], the conventional attribution is followed here. However, omission of Sts 19 from the *A. africanus* hypodigm would not change our conclusions.

This study demonstrates that the morphology of the bony labyrinth has the potential to provide information about both the locomotor behaviour and the phylogenetic relationships of early hominids. Although the labyrinth can only be accessed in fossils by CT scanning, it has the advantage that its morphology can be studied in juvenile specimens because it attains its adult shape and size long before birth. Moreover, relatively large samples are available because petrous pyramids containing an intact labyrinth are common in fossil hominid assemblages. □

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