Proc. Natl. Acad. Sci. USA
Vol. 95, pp. 5417–5419, April 1998
Anthropology, Evolution

The hypoglossal canal and the origin of human vocal behavior

(language evolution/human evolution/*Homo*/*Pan*/*Australopithecus*)

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Communicated by Erik Trinkaus, Washington University, St. Louis, MO, February 19, 1998 (received for review January 5, 1998)

ABSTRACT **The mammalian hypoglossal canal transmits the nerve that supplies the muscles of the tongue. This canal is absolutely and relatively larger in modern humans than it is in the African apes (*Pan* and *Gorilla*). We hypothesize that the human tongue is supplied more richly with motor nerves than are those of living apes and propose that canal size in fossil hominids may provide an indication about the motor coordination of the tongue and reflect the evolution of speech and language. Canals of gracile *Australopithecus*, and possibly *Homo habilis*, fall within the range of extant *Pan* and are significantly smaller than those of modern *Homo*. The canals of Neanderthals and an early "modern" *Homo sapiens* (Skhul 5), as well as of African and European middle Pleistocene *Homo* (Kabwe and Swanscombe), fall within the range of extant *Homo* and are significantly larger than those of *Pan troglodytes*. These anatomical findings suggest that the vocal capabilities of Neanderthals were the same as those of humans today. Furthermore, the vocal abilities of *Australopithecus* were not advanced significantly over those of chimpanzees whereas those of *Homo* may have been essentially modern by at least 400,000 years ago. Thus, human vocal abilities may have appeared much earlier in time than the first archaeological evidence for symbolic behavior.**

Previous Evidence for Language Origins

Language is arguably the most important behavioral attribute that distinguishes humans from other animals. It is indispensable in many complex human social relations, including the planning and coordination of group activities. Language is widely regarded as a prerequisite for deliberative thought and action, self-awareness, or even simple sentience. Because other animals lack language, it is difficult to identify behavioral and anatomical correlates that indicate its first appearance in human evolution. Some have sought to infer language ability from archaeological evidence of subsistence activities that seem to have involved collective decision-making (e.g., big-game hunting) or of structural complexity and diversity in the design of occupation sites (1–4). The appearance of body ornamentation and deliberate burial practices in the late Pleistocene have been identified with consciousness and the awareness of self, thought by some to imply language abilities (5), and the first appearance of unambiguous symbols in the archaeological record, within the last 40,000 years, has been taken by some (1) as marking the first definite evidence for the presence of human language.

Early attempts to infer the presence or absence of human-like speech abilities from such anatomical features of fossil hominids as the presence of a chin or the development of the mylohyoid ridge on the inside of the lower jaw (6, 7) have not been widely credited with success (4, 8). More recently, efforts have been made to reconstruct the shapes of hominid vocal tracts (upper respiratory systems) from bony landmarks of the basicranium (9–12). On the basis of these reconstructions, it has been claimed that Neanderthals and earlier hominids may not have produced the full range of sounds of the sort humans produce today. These claims also have been called into question (4, 13–15). Paleoneurological evidence of language skills has been sought in the presence of brain asymmetries and enlargement in the size of the speech areas of the brain, inferred from the appearance and size of the inside of the braincase (16). Finally, the small size of the thoracic spinal cord, as evidenced by the size of the thoracic vertebral canal, has been proposed as evidence that early *Homo erectus* could not speak (17–19).

The Hypoglossal Canal. One structure that has been neglected in the search for anatomical evidence for the evolution of human vocal abilities is the hypoglossal nerve (cranial nerve XII). This nerve arises from the hypoglossal nucleus of the dorsal medulla of the brain stem and traverses the hypoglossal canal in the basioccipital (20) to supply the motor innervation to all of the intrinsic and all but one of the extrinsic muscles of the tongue. (The sensory innervation of the tongue is provided by other nerves that do not traverse this canal.) It may be hypothesized that the number of motor units in the tongue would be greater in humans than in African apes, allowing finer control of tongue shape in forming speech sounds. Furthermore, if such a size difference in the hypoglossal nerve is reflected in the size of the hypoglossal canal, then the size of the canal will provide evidence about the fineness of innervation of the tongue and serve as an index of the vocal abilities of extant and fossil species.

We studied the cross-sectional areas of hypoglossal canals in adult skulls of extant humans, African apes, and several key fossil hominids. Flexible molding material (President Jet, Coltene AG, Altstatten, Switzerland) was used to make a precise replica of the interior of the canal. Each mold was cut at right angles to its long axis at the point judged to represent the narrowest cross-section. The cross-sectional area of the mold was measured with a microscope fitted with a camera lucida to project a ×12 magnified image onto an electronic drawing tablet connected to a computer running NIH IMAGE version 1.61. The outline of the mold was traced, and the cross-sectional area was calculated.

The mean area of the hypoglossal canal of modern *Homo sapiens* is 1.85 and 2.44 times the cross-sectional areas of the canals of common and pygmy chimpanzees (*Pan troglodytes* and *P. paniscus*, respectively), and 1.33 times that of gorillas (*Gorilla gorilla*) (Figs. 1 and 2; Table 1). In our samples of apes and *H. sapiens*, the range of hypoglossal canal areas of the ape specimens overlaps the lower end of the human range, especially in *Gorilla*. This overlap might be because of the large size, rather than the rich innervation, of the ape tongue. To test this surmise, hypoglossal canal area was size-corrected for the size

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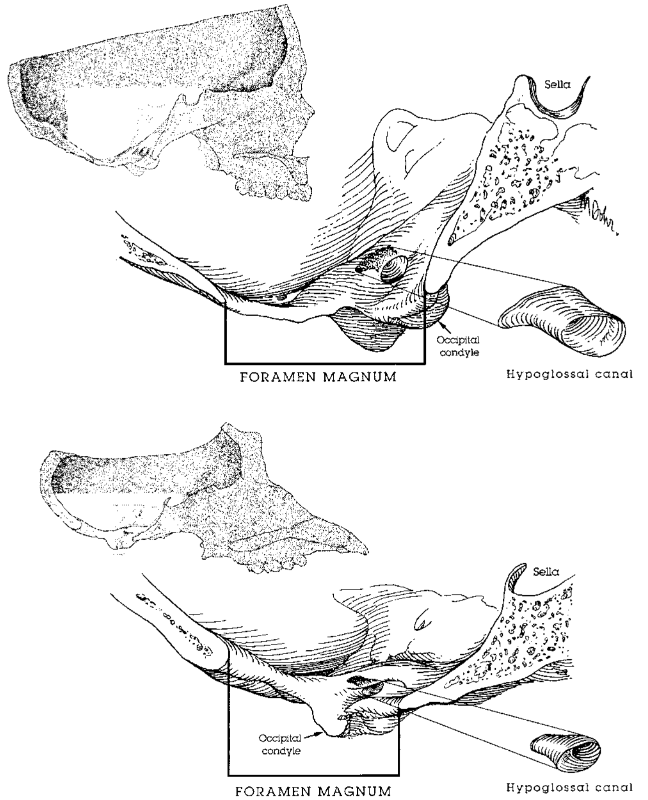

FIG. 1. Anatomy of the bony hypoglossal canal in *H. sapiens* and *P. troglodytes*, viewed from the interior of mid-sagittally sectioned skulls. The shapes of the canals are illustrated at the right, and their anatomical position on the intact skull is shown as unshaded.

of the oral cavity (Fig. 2). The hypoglossal canal is ≈80% (1.8 times) larger relative to the size of the oral cavity in humans than in the apes. Nevertheless, some overlap still occurs between the human and ape samples, perhaps because the size corrector is imperfect or because of variation in all species in the size of structures that run with the nerve through the canal.

In addition to cranial nerve XII, the hypoglossal canal transmits several other small structures, including nutrient arteries for the nerve, a meningeal branch of the ascending pharyngeal artery, and a venous plexus (20). Although it is not known whether the relative sizes of these structures differ in humans and apes, we hypothesize that the canal enlargement seen in *H. sapiens* reflects enlargement of the hypoglossal nerve.

The Antiquity of Speech. We have studied three specimens from the Sterkfontein deposits in South Africa, representing gracile *Australopithecus africanus* [and/or *Homo habilis*, Stw 53 (21–23); Table 2]. The absolute size of these early hominid hypoglossal canals falls below the sampled human range and does not differ significantly from those of either pygmy chimpanzees or common chimpanzees. In contrast, hypoglossal canals of two middle Pleistocene *Homo* (Kabwe, Swanscombe), two Neanderthals (La Chapelle-aux-Saints and La Ferrassie 1), and one early *H. sapiens* (Skhul 5) are well within the size range of modern *H. sapiens* and are significantly larger than those seen in our sample of *P. troglodytes*.

Estimates of the size of the hypoglossal canal relative to that of the oral cavity in the fossils, based on measurements of jaws associated with the sampled occipitals in Skhul 5, La Ferrassie

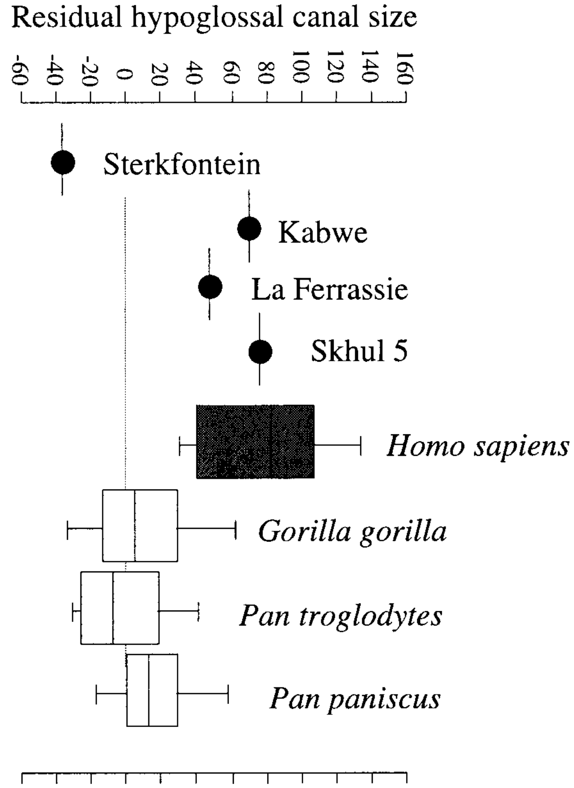

FIG. 2. Box plots of residuals of hypoglossal canal in modern *Homo*, three species of African apes, and the fossil hominids examined. A least-squares regression is fitted to a plot of an independent size variable (log oral cavity size; see Table 1 for definition) against log hypoglossal canal area for the three species and two sexes of *Pan* spp. and *G. gorilla*. Departure of an individual canal area from this regression is expressed as a percentage of expected area. Because the regression is run through the means of ape species and sexes (i.e., n = 6), the mean residual values for those species cluster around 0. The dimensions of the oral cavities of Skhul 5, La Ferrassie, and Kabwe (estimated at 148,936, 123,700, and 149,000 mm^3, respectively) are based on palate dimensions with missing mandibular dimensions reconstructed from maxillary dental arcade length. A single point represents the mean residual hypoglossal canal size for a sample of three Sterkfontein specimens fitted against a single estimate for the oral cavity volume (199 and 244 mm^3) based on dimensions of the following adult specimens from Sterkfontein: Sts 5, 36, 52, Stw 14, 53.

Table 1. Sample statistics for specimens examined

Species	Sex m/f/unkn.	Total specimens	Skull length, mm	Oral cavity volume, mm^3	Hypoglossal canal area, mm^2	SD
Pan troglodytes	17,16,11	44	190.1	113,420	10.26	2.56
Pan paniscus	23,22,7	53	164.1	71,870	7.79	2.31
Gorilla gorilla	15,14,1	30	271.6	242,080	14.28	6.42
*Homo sapiens**	12,11,25	48	184.2	107,240	19.00	6.89

Oral cavity size is the product of palate length × (palate depth + mandible depth) × palate breadth.

*The human sample is comprised of specimens of known sex from the Terry Collection (Smithsonian Institution), miscellaneous specimens of unknown origin in the osteological collections at Duke University, and a small sample of Australians housed at the Peabody Museum, Harvard.

unkn., unknown.

Table 2. Hypoglossal canals of fossil crania compared with the human and ape samples

Specimens	Canal area (mm^2) SD	Compared with *Pan troglodytes*	Compared with *Homo sapiens*
Skhul 5	20.15	$t = 3.80$; $P < 0.0001$	$t = 0.14$; NS
La Ferrassie 1, La Chapelle aux Saints	15.59 (1.16) [16.41 and 14.77, respectively]	$t = 2.05$; $P < 0.01$	$t = 0.49$; NS
Kabwe	19.00	$t = 2.58$; $P < 0.02$	$t = 0.29$; *NS*
Swanscombe	24.52	$t = 5.49$; $P < 0.0001$	$t = 0.79$; NS
Sts 19, Stw 187, Stw 53	9.21 (1.61)	$t = 0.520$; NS	$t = 2.303$; $P < 0.025$

Values are for one-tailed Student's t tests based on comparisons of total, combined-sex samples.
NS, not significant.

1, and Kabwe and on measurements of similar adult specimens from the same site in the Sterkfontein material, yield similar results (Fig. 2): The Pliocene South African hominids resemble African apes, and the other fossil hominids resemble modern *Homo*.

These results suggest minimum and maximum dates for the appearance of the modern human pattern of tongue motor innervation and speech abilities. *A. africanus* and/or *H. habilis* still retained the ape-like pattern, but a human-like hypoglossal canal had evolved by >300,000 years ago [given the estimated ages of Swanscombe (24) and a probably similar one for Kabwe]. If, as we conjecture, the size of the hypoglossal canal reflects the number of motor fibers in the hypoglossal nerve, then human-like speech capabilities may have evolved much earlier than has been inferred from the archaeological evidence for the antiquity of symbolic thought. This hypothesis is consistent with the evidence for accelerated encephalization rates in middle Pleistocene *Homo* (25).

We thank R. J. Clarke, H. Fourie, J.-J. Hublin, R. Kruszynski, A. Langaney, P. Montja, D. R. Pilbeam, C. B. Stringer, F. Thackeray, R. Thorington, Jr., and W. Van Neer for access to specimens and technical assistance and S. Churchill, M. Spencer, E. Trinkaus, and B. A. Williams for helpful comments. Supported by Duke University Research Council.

1. Noble, W. & Davidson, I. (1991) *Man* **26,** 223–253.
2. Mellars, P. (1989) *Curr. Anthrop.* **30,** 349–385.
3. Klein, R. (1989) *The Human Career. Human Biological and Cultural Origins*. (Univ. Chicago Press, Chicago).
4. Schepartz, L. A. (1993) *Yrbk. Phys. Anthrop.* **36,** 91–126.
5. Klein, R. (1995) *J. World Prehist.* **9,** 167–198.
6. Keith, A. (1925) *The Antiquity of Man* (Williams and Norgate, London), 2nd Ed.
7. Walkhoff, O. (1911) *Dtsch. Zahnheilkunde Vorträgen* **22,** 1–71.
8. Vallois, H. (1961) in *Social Life of Early Man*, ed. Washburn, S. L. (Aldine, Chicago), pp. 214–235.
9. Laitman, J. T. & Heimbuch, R. C. (1982) *Am. J. Phys. Anthrop.* **83,** 323–343.
10. Lieberman, P. & Crelin, E. S. (1971) *Linguistic Inquiry* **2,** 203–222.
11. Lieberman, P., Laitman, J. T., Reidenberg, J. S. & Gannon, P. J. (1992) *J. Hum. Evol.* **23,** 447–467.
12. Lieberman, P. (1997) *Uniquely Human: The Evolution of Speech, Thought, and Selfless Behavior* (Harvard Univ. Press, Cambridge, MA).
13. Frayer, D. (1992) *Am J. Phys. Anthropol. Suppl* **14,** 77.
14. Falk, D. (1975) *Am. J. Phys. Anthropol.* **43,** 123–132.
15. Heim, J.-L. (1989) *Bull. Mem. Soc. Anthropol. (Paris)* **1,** 95–118.
16. Deacon, T. C. (1992) in *Language Origins: A Multidisciplinary Approach*, ed. Wind, J. (Kluwer, Dordrecht, The Netherlands), pp. 121–162.
17. Walker, A. & Shipman, P. (1996) *The Wisdom of the Bones* (Knopf, New York).
18. Walker, A. (1993) in *The Nariokotome Homo erectus Skeleton*, eds. Walker, A. & Leakey, R. (Harvard Univ. Press, Cambridge, MA), pp. 411–432.
19. MacLarnon, A. (1993) in *The Nariokotome Homo erectus Skeleton*, eds. Walker, A. & Leakey, R. (Harvard Univ. Press, Cambridge, MA), pp. 359–390.
20. Williams, P. L. & Warwick, R. (1980) *Gray's Anatomy* (Churchill, Livingston, London), 36th ed.
21. Wolpoff, M. (1996) *Human Evolution* (McGraw–Hill, New York).
22. Clarke, R. J. (1985) in *Hominid Evolution: Past, Present, and Future*, ed. Tobias, P. V. (Liss, New York), pp. 287–298.
23. Hughes, A. R. & Tobias, P. V. (1977) *Nature (London)* **265,** 310–312.
24. Bridgland, D. R. (1994) *The Quaternary of the Thames* (Chapman & Hall, London).
25. Ruff, C. B., Trinkaus, E. & Holliday, T. W. (1997) *Nature (London)* **387,** 173–176.