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Hypoglossal canal size and hominid speech

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ABSTRACT **The mammalian hypoglossal canal transmits the nerve that supplies the motor innervation to the tongue. Hypoglossal canal size has previously been used to date the origin of human-like speech capabilities to at least 400,000 years ago and to assign modern human vocal abilities to Neandertals. These conclusions are based on the hypothesis that the size of the hypoglossal canal is indicative of speech capabilities. This hypothesis is falsified here by the finding of numerous nonhuman primate taxa that have hypoglossal canals in the modern human size range, both absolutely and relative to oral cavity volume. Specimens of *Australopithecus afarensis*, *Australopithecus africanus*, and *Australopithecus boisei* also have hypoglossal canals that, both absolutely and relative to oral cavity volume, are equal in size to those of modern humans. The basis for the hypothesis that hypoglossal canal size is indicative of speech was the assumption that hypoglossal canal size is correlated with hypoglossal nerve size, which in turn is related to tongue function. This assumption is probably incorrect, as we found no apparent correlation between the size of the hypoglossal nerve, or the number of axons it contains, and the size of the hypoglossal canal in a sample of cadavers. Our data demonstrate that the size of the hypoglossal canal does not reflect vocal capabilities or language usage. Thus the date of origin for human language and the speech capabilities of Neandertals remain open questions.**

The size of the hypoglossal canal has been linked with the evolution of language and used to date the origin of human speech to at least 400,000 years ago by Kay *et al*. (1). This linkage is based on the fact that the hypoglossal canal of the occipital bone contains cranial nerve XII, which supplies the motor innervation to the intrinsic muscles of the tongue and all but one of the extrinsic muscles (2). Because the hypoglossal canals of two Neandertal specimens are within the modern human size range, it has been suggested that Neandertals had vocal capabilities equivalent to those of modern humans (1). Despite quick popular acceptance (3), the hypothesized link between hypoglossal canal size and speech remains untested. Instead, it has been assumed that the size of the hypoglossal nerve is related to speech, and that the size of the hypoglossal canal is correlated with the size of the hypoglossal nerve (1). The finding that modern humans ($n = 48$) have larger hypoglossal canals than most chimpanzees and gorillas (1) does not test these hypotheses.

To test the hypothesis that hypoglossal canal size is indicative of speech, we measured the hypoglossal canals of 75 nonhuman primates and 104 modern humans. If the size of the hypoglossal canal can be used as an indicator of speech, then it should be larger (either absolutely or relative to tongue mass) in humans than in other primates. We also measured the hypoglossal canal in specimens of the early hominid taxa *Australopithecus afarensis* and *Australopithecus boisei* to further assess the evolution of canal size. To test the assumption that hypoglossal canal size is correlated with hypoglossal nerve size and that the latter reflects the number of axons in the nerve, we measured both nerve and canal diameter and estimated axon number in a sample of human cadavers.

MATERIALS AND METHODS

Materials. The modern human skeletal sample ($n = 104$) was drawn from the Laboratory for Human Evolutionary Studies (University of California, Berkeley) and the Atkinson Collection (University of the Pacific School of Dentistry). These collections contain skulls of both sexes and represent a variety of populations, but no reliable information on geographic origin or sex is available for most individuals. Of the 104 human skulls, 75 were selected without regard to canal size. A further 29 were chosen to represent the extremes of variation (both small and large). From these 104 individuals, 141 different canals (left and right sides) were molded. The 75 nonhuman primate specimens are from the Museum of Vertebrate Zoology (University of California, Berkeley) and the Laboratory for Human Evolutionary Studies and were selected in an *ad hoc* fashion. From these 75 individuals, 123 different canals were molded. Only adult crania with no indications of pathology were used for both the human and nonhuman primate samples. We observed a number of canals that were partially or fully bifurcated (4, 5). No canals with any trace of bifurcation were included in the skeletal portion of this study, as previous work suggests that bifurcated canals tend to be smaller in volume (6).

Molds of the hypoglossal canal in fossil hominids were obtained from original specimens. The hypoglossal canals had been fully cleaned some years ago, so no canals were "cleaned" (i.e., created) for this project. The human cadaver sample comprises five nerve-canal pairs from five individuals (three females, two males). The cadavers are Americans of European ancestry with no known history or indication of neuropathology. The nerves used were well preserved both macroscopically and microscopically. Although soft tissue structures can change in size post mortem, all cadavers we used have roughly the same date of death and were examined at the same time. The possibility of shrinkage is inherent in any use of embalmed cadaver material, but because all the samples were prepared in the same way, any shrinkage should be consistent across the sample and thus not confound any correlations. Furthermore, the number of axons contained within the nerve would not be altered by postmortem shrinkage.

Methods. Molds of the interior of the hypoglossal canal were made with the same flexible molding material (President Jet, Coltene, Switzerland) employed by Kay *et al.* (1). The molds were sectioned at right angles to their long axis at the point judged to represent the narrowest cross section (1). We digitized cross sections of 20 canal molds three times, using both a flatbed scanner (1,200 dots per inch) and a microscope

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equipped with a digital camera (1,600 dots per inch). The cross-sectional area was then measured with NIH Object Image version 1.62n3. The flatbed scanner method was more than twice as precise as the microscope method (error of 1.3% versus 2.8%). Placing the sectioned molds on the flat surface of the scanner guarantees that the plane of the cross section is parallel to the optics, which is difficult to achieve with a microscope. The entire sample was then measured by the flatbed scanner method. Ten canals were molded twice, and the resulting measurements show a mean error of 5.3% (range of 1.1% to 9.5%) for the entire process. All molds were sectioned and measured by one person, who was unaware of their source and taxonomic identity.

Projecting an irregular solid, such as a mold of the hypoglossal canal, into two dimensions can result in an inflated "cross-sectional" area. We painted the cross sections white (contrasting with the blue of the rest of the mold) on all molds to eliminate this type of error. The thresholding function of NIH Object Image was then used to discriminate between the actual cross section and projections of other portions of the mold. Ten cross sections were measured unpainted, then painted and remeasured to illustrate the effect of failing to account for this type of error. The unpainted measurement was greater than the painted measurement in each case, with a mean increase of 19%.

Kay *et al.* (1) considered their hypoglossal canal areas relative to oral cavity size [palate length × (palate depth + mandible depth) × palate breadth] in an attempt to correct for tongue size. However, studies have demonstrated that there is no correlation between oral skeletal dimensions and tongue volume in living humans (7). Studies of several human populations have similarly not found any correlation between oral cavity volume and tongue volume (8–10).

The significant bilateral variation in hypoglossal canal area seen in some individuals, with one canal sometimes twice the size of the other, also indicates that canal size does not scale with oral cavity size. The mean percentage difference between the left and right hypoglossal canal areas is 24% in our human sample ($n = 37$ pairs, right side on average 8.1% larger, which is not significant) and 21% in the nonhuman primate sample ($n = 48$ pairs, left side on average 1.7% larger, which is not significant).

We measured oral cavity size and palate size (to allow specimens without mandibles to be included) in our skeletal sample. When Pearson's correlation coefficient is used, oral cavity size is significantly correlated with palate size ($r = 0.95$, $P < 0.0001$, $n = 101$), but neither of these measures is correlated with hypoglossal canal size in our modern human sample ($r = 0.02, P = 0.82, n = 101$ for oral cavity size; $r = 0.05$, $P = 0.58, n = 141$ for palate size). In the entire skeletal sample (human and nonhuman), both oral cavity size ($r = 0.47$) and palate size ($r = 0.51$) are somewhat correlated with canal area. However, examination of the partial correlation matrix reveals that this is an effect of skull breadth (oral cavity size $r = 0.13$, palate size $r = -0.10$, skull breadth $r = 0.50$). On the basis of the studies of living humans (7–10), the bilateral variation, and the lack of clear correlations, we conclude that it is not appropriate to use oral cavity size or palate size as a correction factor for hypoglossal canal area, though we do so below to allow full comparison with the results of Kay *et al.* (1).

The cross-sectional area of the hypoglossal canals of the human cadavers were measured as above after removal of the hypoglossal nerve and chemical defleshing of the bone. The portion of the hypoglossal nerve that runs through the hypoglossal canal was removed from the cadavers. About 3 mm of nerve was discarded from each end to ensure that only the intracanal portion of the nerve was analyzed. Care was taken to collect all of the nerve fascicles for analysis, as the rootlets extending from the brainstem to form the hypoglossal nerve do not always unite before entering the canal. The nerves were placed in 10% formalin, dehydrated, infiltrated, and embedded in paraffin by using an automated tissue processor. The blocks were then sectioned at right angles to the long axis of the nerve. At 0.5-mm intervals along the nerve, 10–15 serial sections (thickness = 10 μm) were mounted on microscope slides and stained with toluidine blue O.

The sections were visualized at ×40 magnification under a compound microscope equipped with a digital camera (2,400 dots per inch). Five to 10 consecutive undamaged sections were digitized at ≈1.0-mm intervals along each nerve fascicle, and their area was measured by using Image Pro 2.0 (Media Cybernetics). The mean of each 5- to 10-section "set" (the "set mean") was calculated. Then, for each hypoglossal nerve (or set of fascicles), three values were obtained: the overall mean

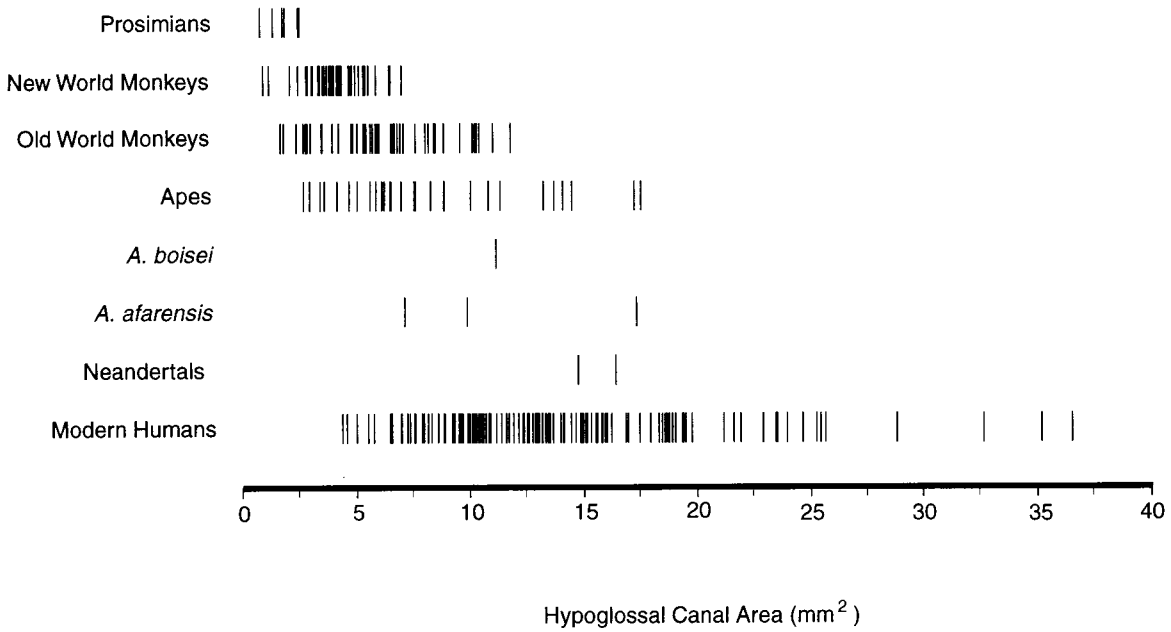

FIG. 1. Plot of hypoglossal canal cross-sectional areas. All data are from the present study except the Neandertal measurements (La Chapelle aux Saints, La Ferrassie 1), which are from Kay *et al.* (1).

Table 1. Hypoglossal canal cross-sectional areas for modern specimens examined

Taxon	No. of individuals	No. of canals	Hypoglossal canal area, mm^2			Canal area/palate size ($\times 10^{-4}$)			Canal area/oral cavity size ($\times 10^{-4}$)		
			Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Homo sapiens	104	141	4.4–36.5	13.8	6.1	1.7–18.7	5.1	2.9	0.6–5.8	1.8	1.0
Pan troglodytes	6	11	5.8–14.5	9.1	3.2	1.0–7.4	3.8	2.1	0.4–2.5	1.3	0.6
Gorilla gorilla	5	7	8.3–17.5	12.7	3.8	0.9–3.9	2.1	1.0	0.3–1.3	0.7	0.3
Pongo pygmaeus	2	3	3.4–5.6	4.2	1.2	2.9–4.8	3.6	1.1	0.8–1.1	0.9	0.2
Hylobates lar	3	4	4.1–6.1	5.0	0.8	8.6–12.7	10.4	1.7	3.2–4.8	3.9	0.7
Hylobates moloch	2	3	2.7–6.9	4.2	2.4	4.0–20.4	9.6	9.4	1.9–7.2	3.7	3.0
Cercopithecus aethiops	1	1	1.7	—	—	7.9	—	—	2.5	—	—
Cercopithecus neglectus	1	2	2.8–3.0	2.9	0.1	3.6–3.8	3.7	0.2	1.2–1.3	1.2	0.1
Cercopithecus talapoin	1	2	1.6–2.3	2.0	0.5	14.5–20.8	17.7	4.5	4.5–6.5	5.5	1.4
Colobus badius	1	2	3.9–4.2	4.1	0.2	22.2–23.7	23.0	1.1	6.5–7.0	6.8	0.3
Colobus polykomos	1	1	6.5	—	—	6.6	—	—	2.1	—	—
Erythrocebus patas	1	2	4.2–5.4	4.8	0.9	11.0–14.2	12.6	2.3	3.5–4.6	4.1	0.7
Macaca sp.	1	2	5.3–5.6	5.5	0.2	6.4–6.8	6.6	0.3	1.8–1.9	1.9	0.1
Macaca fascicularis	1	2	2.6–2.8	2.7	0.1	4.1–4.4	4.2	0.2	1.3–1.4	1.3	0.1
Macaca maurus	1	2	4.8–5.0	4.9	0.1	4.0–4.1	4.0	0.1	1.2–1.2	1.2	0.0
Macaca mulatta	2	4	1.7–10.1	6.1	3.4	4.3–13.7	8.1	4.2	1.1–3.5	2.2	1.1
Macaca nemestrina	1	2	5.8–6.8	6.3	0.7	2.6–3.1	2.9	0.3	0.9–1.0	1.0	0.1
Macaca nigra	1	1	6.9	—	—	2.9	—	—	1.0	—	—
Mandrillus sphinx	1	2	6.6–8.5	7.5	1.3	9.0–11.6	10.3	1.8	1.9–2.4	2.1	0.4
Papio sp.	1	2	8.4–8.5	8.4	0.1	1.8–1.8	1.8	0.0	0.5	0.5	0.0
Papio anubis	3	6	4.8–10.3	7.1	2.3	2.2–4.3	3.0	0.9	0.6–1.1	0.8	0.2
Papio ursinus	6	11	5.9–11.8	8.7	1.9	2.3–8.4	4.1	2.1	0.7–2.3	1.1	0.6
Presbytis sp.	1	1	3.4	—	—	6.4	—	—	2.0	—	—
Presbytis entelleus	1	2	2.8–3.5	3.2	0.5	3.9–4.9	4.4	0.7	1.2–1.5	1.4	0.2
Theropithecus gelada	1	1	2.7	—	—	1.0	—	—	0.3	—	—
Alouatta palliata	12	16	2.8–7.0	4.6	1.1	4.7–11.4	7.6	2.4	1.3–3.3	2.0	0.6
Aotus vociferans	2	3	0.9–2.1	1.4	0.6	15.2–30.5	20.9	8.4	3.2–7.9	5.1	2.4
Ateles geoffroyi	4	7	2.4–4.0	3.4	0.6	6.3–10.3	7.6	1.5	1.9–2.7	2.2	0.3
Cebus albifrons	1	2	4.3–4.3	4.3	0.0	10.8–10.9	10.8	0.0	3.0–3.0	3.0	0.0
Cebus apella	2	3	2.8–3.5	2.3	0.4	9.5–12.0	8.0	1.3	2.9–3.4	2.3	0.2
Cebus capucinus	6	10	3.3–6.5	4.8	1.0	10.0–18.5	14.2	2.9	—	—	—
Nycticebus coucang	1	2	2.4–2.5	2.5	0.0	32.2–32.5	32.6	0.6	7.4–7.6	7.5	0.1
Perodicticus potto	2	4	0.8–1.8	1.4	0.5	15.0–36.0	24.6	9.0	3.1–7.4	5.7	2.0

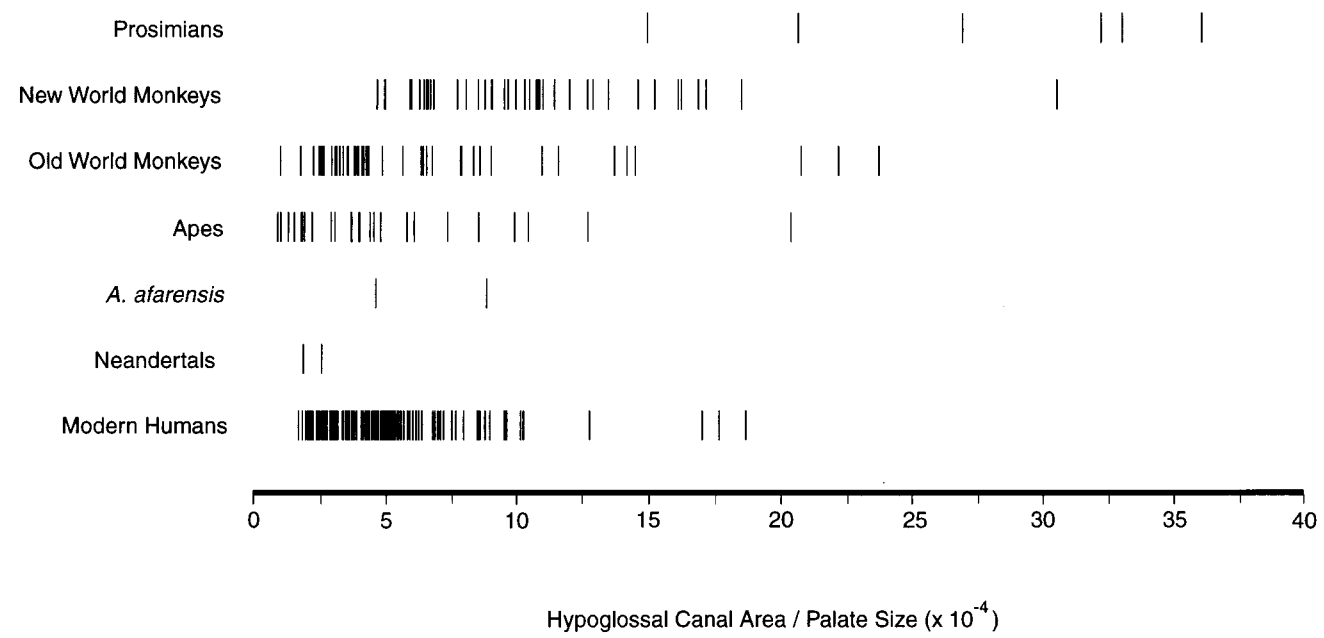

FIG. 2. Plot of hypoglossal canal cross-sectional areas relative to palate size (palate length × palate breadth × palate depth). The distributions are almost the same if oral cavity size is used instead of palate size (the two are correlated at a level of 0.95), but the sample size is smaller because some specimens lack mandibles. The Neandertal palate sizes (La Chapelle aux Saints, La Ferrassie 1) were measured on casts, and so are approximate values only. The palate size of the La Chapelle specimen is almost certainly artificially low because of alveolar resorption (i.e., the point should likely be even further to the left on the plot).

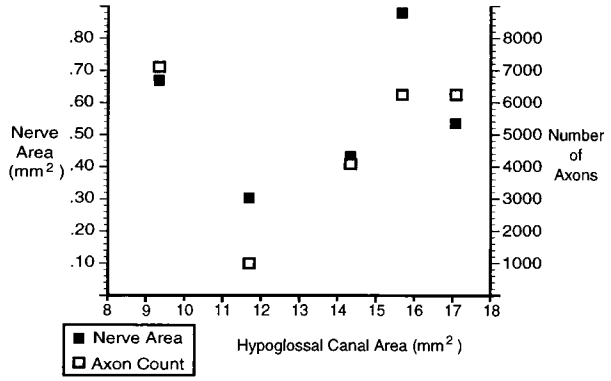

FIG. 3. Plot of mean hypoglossal nerve cross-sectional area and axon number versus mean hypoglossal canal cross-sectional area.

area, the minimum area, and the maximum area. The minimums and maximums refer to the "set means," not to measurements of individual nerve sections. Generally, there was some variation in the cross-sectional areas of the fascicles making up the nerve between widely separated sets (on the order of 10–20%), but little between neighboring sets and almost none within the sets. The number of axons in each nerve was estimated by two-dimensional stereology (11). The axon density for each fascicle, based on a counting frame (0.005 mm^2) on five different nerve sections, was multiplied by the mean cross-sectional area of that fascicle. The fascicle totals were then summed to provide the nerve total.

RESULTS

Extant Taxa. We examined the cross-sectional area of the hypoglossal canal in a variety of nonhuman primate taxa to test the hypothesized link between canal size and speech. Because nonhuman primates are not known to speak, their hypoglossal canals should be smaller than those of modern humans if Kay *et al.*'s (1) use of canal size to infer speech is valid. In fact, many nonhuman primate specimens (70 canals in 44 individuals) have hypoglossal canal areas that fall within the range of our modern human sample (Fig. 1; Table 1). Scaled for oral cavity size, almost all of the nonhuman canals fall within the human range (107 of 123 canals, 65 of 75 individuals; Fig. 2). A total of 64 canals from 40 nonhuman primates are within the modern human size range both absolutely and after correction for oral cavity size.

Modern humans have a larger mean hypoglossal canal area than the other primate taxa measured, but not when corrected for oral cavity size (Table 1). In any case, the argument that hypoglossal canal area can be used to infer speech hinges on the *range* of areas, rather than the mean, since an individual's mechanical ability to speak can depend only on its own canal size, not the mean size for its species.

To examine the postulated functional basis for the linkage between hypoglossal canal size and speech, we investigated the assumption that hypoglossal canal size is correlated with hypoglossal nerve size in five nerve–canal pairs from five human cadavers. The cross-sectional area of the hypoglossal nerve was measured in each individual, along with the cross-sectional area of the corresponding hypoglossal canal that contained the nerve. A visual comparison of the relationship between canal area and mean nerve size (Fig. 3) illustrates the general lack of correlation between the two ($r = 0.19$, $P = 0.79$). The cross-sectional area of the nerve varies somewhat along its length, but there is no correlation between canal area and the minimum nerve area ($r = 0.14$, $P = 0.4$) or the maximum nerve area ($r = 0.21$, $P = 0.76$). The lack of a significant correlation was confirmed by Spearman's rank correlation test ($\rho = 0.20$, $P = 0.69$). Although the number of separate nerve bundles composing the hypoglossal nerve in the canal varied from one to four, there was no apparent correspondence between number of bundles and overall size. Given the small sample size, our data do not exclude the possibility of a correlation between nerve size and canal size, but they do indicate that such a correlation cannot be assumed.

The ability of the hypoglossal nerve to transmit information depends on the nerve fibers it contains, rather than its overall size per se (2). We therefore examined whether a correlation existed between the number of axons in the hypoglossal nerve, which is known to vary in humans (12), and the size of the hypoglossal canal in our cadaver sample. There appears to be no significant correlation ($r = 0.16$, $P = 0.82$) in our sample of five individuals (Fig. 3). If the axon count (or any other feature of the nerve) is not correlated with the morphology of the bony canal, then such data are not applicable to studies of extinct taxa.

Fossil Taxa. Kay *et al.* (1) state that the hypoglossal canals of *Australopithecus africanus* (Stw 19, Stw 187), and possibly *Homo habilis* (Stw 53), are significantly smaller than those of modern humans. On this basis, they conclude that the vocal abilities of *Australopithecus* were not advanced significantly over those of chimpanzees. They report a mean canal area of 9.21 mm^2 (SD 1.61) for the three Sterkfontein (Stw) specimens they examined. This mean is well within the range of our modern human sample (4.35–36.50 mm^2), even when corrected for oral cavity size. If one of the Sterkfontein specimens were three standard deviations below the reported mean, it would still be in the size range of our modern human sample.

To further investigate hypoglossal canal size in fossil hominids, we obtained molds of the hypoglossal canals in four specimens of *Australopithecus*: three specimens of *Australopithecus afarensis* (adult A.L. 333-45 and the immature A.L. 333-105 and A.L. 333-114) dated at 3.20 million years ago (13) and one immature *Australopithecus boisei* specimen (Omo L338-y-6) dated at 2.39 million years ago (14, 15). The canals of the immature specimens are fully formed and completely ossified. The adult specimen A.L. 333-45 preserves about 85% of the hypoglossal canal. The remainder was reconstructed two separate times, using a straight line connecting the free edges of the canal to produce a minimum canal size. Two molds were also obtained from the other fossil hominid canals, and the minimum areas are reported in Table 2. All these specimens

Table 2. Measurements for *Australopithecus* specimens

Taxon	Age stage	Specimen	Hypoglossal canal area,* mm^2	Canal area/ palate size ($\times 10^{-4}$)	Canal area/ oral cavity size ($\times 10^{-4}$)
A. afarensis	Adult	A.L. 333-45 (recon.)†	17.3	4.6	1.2
A. afarensis	Immature	A.L. 333-105	9.9	8.9	—
A. afarensis	Immature	A.L. 333-114	7.1	—	—
A. boisei	Immature	Omo L338-y-6 (right)	11.1	—	—

*Canals were molded twice and the minimum value is reported.
†Palate and oral cavity size were calculated by using the composite reconstructed *A. afarensis* cranium, which may underestimate the palate size for A.L. 333-45.

have hypoglossal canal areas that are within the size range of our modern human sample, both absolutely and after correction (when possible) for palate or oral cavity size. The immature *A. boisei* canal and one of the immature *A. afarensis* canals are near the middle of the (adult) modern human range, and the adult *A. afarensis* canal is notably larger than the human mean (Fig. 2). According to the criteria of Kay *et al.* (1), then, modern human speech capabilities originated at least 3.2 million years ago in *Australopithecus afarensis*, a species not previously noted for encephalization, symbolic capacity, or even stone tool making.

CONCLUSIONS

Many nonhuman primate specimens have hypoglossal canals that are absolutely and relatively within the size range of modern humans. The hypoglossal canals of *Australopithecus afarensis*, *A. boisei*, and *A. africanus* are also within the modern human size range. The size of the hypoglossal nerve and the number of axons it contains do not appear to be significantly correlated with the size of the hypoglossal canal. We conclude that the size of the hypoglossal canal is not a reliable indicator of speech. Therefore the timing of the origin of human language and the speech capabilities of Neandertals remain open questions.

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