

Early hominin auditory capacities

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Studies of sensory capacities in past life forms have offered new insights into their adaptations and lifeways. Audition is particularly amenable to study in fossils because it is strongly related to physical properties that can be approached through their skeletal structures. We have studied the anatomy of the outer and middle ear in the early hominin taxa *Australopithecus africanus* and *Paranthropus robustus* and estimated their auditory capacities. Compared with chimpanzees, the early hominin taxa are derived toward modern humans in their slightly shorter and wider external auditory canal, smaller tympanic membrane, and lower malleus/incus lever ratio, but they remain primitive in the small size of their stapes footplate. Compared with chimpanzees, both early hominin taxa show a heightened sensitivity to frequencies between 1.5 and 3.5 kHz and an occupied band of maximum sensitivity that is shifted toward slightly higher frequencies. The results have implications for sensory ecology and communication, and suggest that the early hominin auditory pattern may have facilitated an increased emphasis on short-range vocal communication in open habitats.

INTRODUCTION

Audition is related to basic aspects of an organism's survival, particularly localization of sound sources (1), including potential dangers in the environment, and acoustic communication (2). Studies of hearing in living primates have revealed patterns of variation that largely follow the major taxonomic subdivisions within the order Primates, with strepsirrhines generally showing greater high-frequency sensitivity and haplorhines (including chimpanzees) showing increasing sensitivity to lower frequencies (1, 3, 4). Comparative genomic studies have revealed changes during the course of our own evolutionary history in several genes related to the development of the auditory structures (5) and hearing (6). At the same time, there are clear anatomical differences in the ear between humans and chimpanzees (7–10), and auditory differences have been reported (3, 11, 12). Thus, it would be of interest to reconstruct the auditory capacities of our fossil human ancestors.

Of all the special senses, audition is particularly amenable to study in fossils because it is strongly related to physical properties that can be approached through their skeletal structures (13–15). Previously, it was shown that the anatomy of the outer and middle ear has a strong influence on the auditory capacities in fossil hominins (14, 15). These

previous studies applied a comprehensive model of the outer and middle ear to the Middle Pleistocene hominins from the site of the Sima de los Huesos (Sierra de Atapuerca, Spain) and showed them to have similar auditory capacities as living humans, being clearly different from chimpanzees. The results were argued to have implications for the evolution of language. In addition, studies into the sensory ecology of primates (16–20) represent an emerging field of inquiry that is providing new insights into their adaptations. Given the importance of understanding sensory ecology and communication in early hominins, we have studied the skeletal structures of the ear and reconstructed the auditory capacities in several early hominin individuals from the South African Plio-Pleistocene sites of Sterkfontein and Swartkrans, respectively.

Some anatomical differences from modern humans in the outer and middle ear have been reported (21–26). Specifically, Rak and Clarke (24) argued that both *Australopithecus africanus* and *Paranthropus robustus* show a mediolaterally elongated external auditory canal (EAC). In addition, *P. robustus* was characterized as showing some possibly derived features, including a trumpet-shaped EAC (being wider laterally and narrower medially) and a smooth and shallow tympanic sulcus (the insertion for the tympanic membrane). The tympanic cavity itself is described as spacious, with a large, inflated promontory on the medial wall and a pronounced promontory sulcus. In these latter two features, this taxon is argued to be most similar to recent humans. The promontory reflects the projection of the basal turn of the cochlea, and a more projecting promontory might imply a larger cochlea. However, the radius of the basal turn in *P. robustus* is similar in size to chimpanzees (10).

Regarding the ear ossicles, the malleus in both *A. africanus* and *P. robustus* is derived and human-like in its proportions, and distinct from chimpanzees (26). In contrast, Rak (22, 23) has argued for a highly specialized anatomy of the incus in *P. robustus*. However, the discovery of a second, complete incus from this taxon suggests that some degree of variation is present, and the anatomical details of both specimens seem to fall within that of extant hominids, most closely resembling chimpanzees in size and proportions (26). Whereas no incus is currently known for *A. africanus*, *P. robustus* shows a unique combination of a human-like malleus and ape-like incus. The resulting malleus/incus lever ratio

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in *P. robustus* is intermediate between the higher values in chimpanzees and gorillas, and the low values in humans (7, 26). The stapes in *A. africanus* was argued to resemble chimpanzees in its overall size, including the small size of the footplate (25). Although a more recent study suggested larger stapes footplates in early hominins (21), the discovery of additional stapes from both *A. africanus* and *P. robustus* has confirmed their small dimensions (26). Thus, the early hominins seem to be characterized by a human-like malleus, whereas the incus and stapes are primitive and most similar to those of chimpanzees in their size and shape (25, 26). Although not definitive, these differences in the ear ossicles in early hominins are consistent with somewhat different auditory capacities than in living humans.

Previous studies of the inner ear in early hominin taxa have provided insights into their taxonomic relationships and locomotion (10, 21, 27). Although most analyses have focused on the semicircular canals, the cochlear basal turn is similar in size in chimpanzees and early hominins, but slightly larger in recent humans. Nevertheless, little inference regarding hearing abilities can be drawn from these limited data. In addition, the length of the cochlea along the outer surface has been measured in several early hominin specimens, and was found to be shorter than in modern humans (21). If this is taken as a proxy measure for the length of the bony spiral lamina, it may indicate a shorter basilar membrane length in the early hominins. This shorter length would be consistent with a higher high-frequency cutoff (28), above the ca. 20-kHz cutoff in humans, perhaps resembling chimpanzees (ca. 30-kHz cutoff) more closely (29). Thus, on anatomical grounds, there appear to be several lines of evidence suggesting that early hominins may have differed in their auditory capacities from living humans.

To address this question more directly, we have studied the skeletal structures of the outer and middle ear and modeled the auditory capacities in several early hominin individuals, chimpanzees, and modern humans (see Materials and Methods and the Supplementary Materials). To measure the anatomical variables of the outer and middle ear (Fig. 1), we relied mainly on virtual [three-dimensional (3D) computed tomography (CT)] reconstructions, complemented by direct measurements on other specimens where these anatomical regions are exposed (see Materials and Methods and the Supplementary Materials; fig. S1). Subsequently, we modeled the pattern of sound power transmission through the outer and middle ear up to 5.0 kHz in several of the most complete early hominin individuals, as well as in chimpanzees and modern humans (see Materials and Methods and the Supplementary Materials; figs. S2 to S12 and tables S1 to S3). The model includes a number of skeletal variables (Fig. 1) that can be measured in fossil specimens and considers the function of each of the components of the outer and middle ear, their acoustic and mechanical properties, and the way in which they interact (30). The soft tissue variables that cannot be measured in fossil specimens were held constant in the model for all taxa.

Although our results are not a true audiogram, there is a strong correlation between sound power transmission through the outer and middle ear and auditory sensitivity to different frequencies (31–33). Indeed, our results for sound power transmission in the modern human and chimpanzee comparative samples agree with the published audiograms for these species (see below). Thus, it is reasonable to conclude that the skeletal differences between humans and chimpanzees can explain an important part of the interspecific differences in their patterns of sound power transmission in the outer and middle ear. Therefore, these skeletal differences can be

used to approach the auditory capacities in closely related fossil hominin species.

RESULTS

Skeletal structures of the ear

Our measurements of the skeletal structures of the outer and middle ear in chimpanzees and humans (Table 1) are compatible with the scattered data previously reported by different researchers using a variety of measurement techniques and disparate samples (see the Supplementary Materials; table S4). Chimpanzees and humans showed significant differences in all of the anatomical variables measured in the present study except for the volume of the tympanic cavity (V_{MEC}), the size of the stapes footplate (A_{FP}), and the mass of the stapes (M_S) (Tables 1 and 2). The lack of significant differences in the stapes variables may be due to the slightly smaller sample sizes than the other variables, because other studies based on much larger sample sizes have shown that humans are characterized by larger stapes footplates than chimpanzees (7, 34), and heavier masses for the stapes as well (35–37).

We have limited the statistical comparisons between the early hominins and extant taxa to those variables with a valid $n > 3$ in each taxon. Compared with chimpanzees, *A. africanus* showed significant differences in four of six skeletal variables (Tables 1 and 2), including the length (L_{EAC}) and cross-sectional area (A_{EAC}) of the EAC and the areas of the tympanic membrane (A_{TM}) and stapes footplate (A_{FP}). No difference was found in either the volume of the tympanic cavity or the radius of the entrance to the aditus. It was possible to compare fewer variables in *P. robustus*, but this taxon showed significant differences from chimpanzees in three out of four variables, including the length (L_{EAC}) and cross-sectional area (A_{EAC}) of the EAC and the area of the tympanic membrane (A_{TM}). However, there was no difference in the size of the stapes footplate.

Compared with humans, *A. africanus* showed significant differences in three of six skeletal variables (Tables 1 and 2), including the volume of the tympanic cavity (V_{MEC}), the length of the EAC (L_{EAC}), and the stapes footplate area (A_{FP}). Again, fewer variables can be compared for *P. robustus*, but this taxon showed significant differences from humans in three of four variables, including the length (L_{EAC}) and cross-sectional area (A_{EAC}) of the EAC and the area of the stapes footplate (A_{FP}).

Direct comparison between the two early hominin taxa *A. africanus* and *P. robustus* was limited to just four variables with sample size of $n > 3$. Significant differences were found in the areas of the tympanic membrane (A_{TM}) and stapes footplate (A_{FP}), with both being larger in *P. robustus*.

Our data for the early hominins, then, have confirmed that both *A. africanus* and *P. robustus* are characterized by an EAC that is intermediate in length between humans and chimpanzees. However, contrary to previous suggestions (24), the EAC in *P. robustus* does not appear to be more trumpet-shaped than that of other hominin species, and some degree of trumpet shape seems to characterize the EAC in all hominin taxa, with the narrowest portion of the EAC generally being located medially, close to the tympanic membrane. At the same time, the cross-sectional area of the EAC is enlarged and human-like in both early hominin taxa. The volume of the tympanic cavity is smallest in *A. africanus*. In contrast, although not examined statistically, the mean volume of the tympanic cavity in *P. robustus* is similar to both the chimpanzee and modern human means. The volume of the mastoid air cells shows a large degree of intraspecific variation in

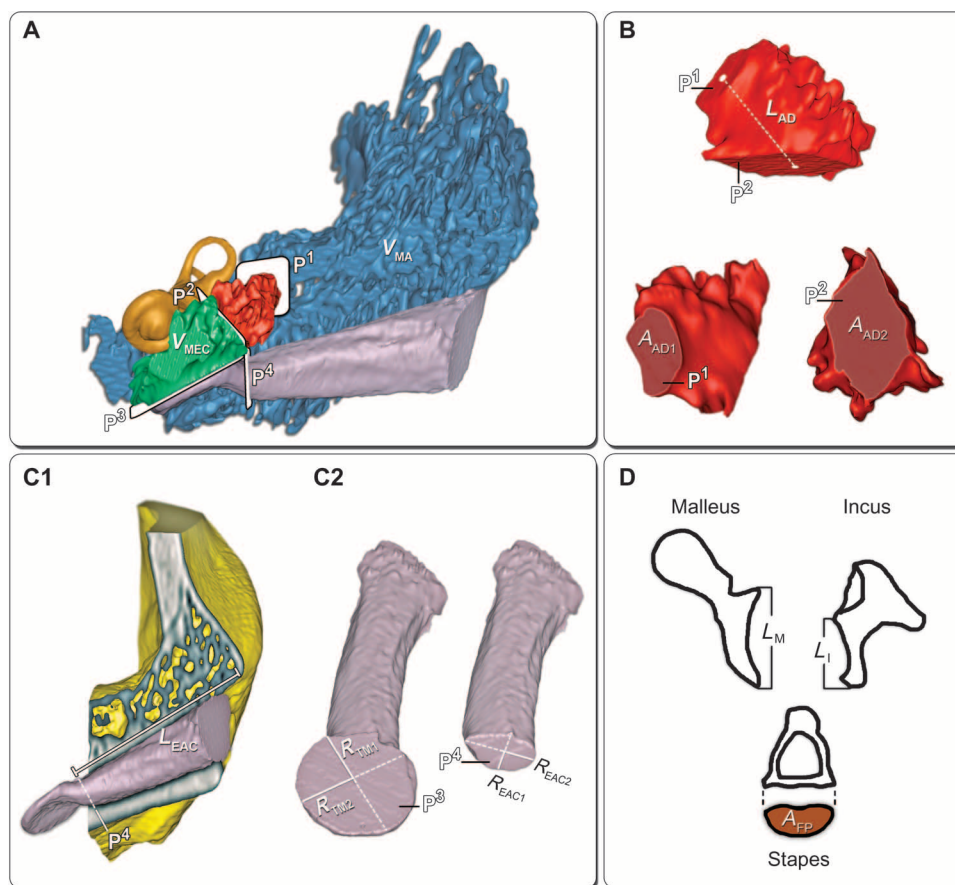


Fig. 1. Measurements of the middle and outer ear (A to C) and ear ossicles (D). (A), (B), (C1), (C2), and (D) are not drawn to the same scale. (A) to (C) are based on the 3D reconstruction of the left side of HTB 1769 (*Pan troglodytes*), showing the EAC (gray), the middle ear cavity (green), the aditus ad antrum (red), the mastoid antrum and connected mastoid air cells (blue), the inner ear (orange), and the temporal bone (yellow). P^1 , limit between the mastoid antrum and the connected mastoid air cells with the aditus ad antrum. P^2 , entrance to the aditus ad antrum from the middle ear cavity. P^3 , medial edge of the tympanic groove (sulcus tympanicus). P^4 , cross section perpendicular to the long axis of the EAC that meets the lateral end of the tympanic groove. (A) V_{MA} , volume of the mastoid antrum and connected mastoid air cells, measured dorsal to P^1 ; V_{MEC} , volume of the middle ear cavity, bounded by P^2 to P^3 . (B) L_{AD} , length of the aditus ad antrum, measured as the distance from the center of P^1 to the center of P^2 ; A_{AD1} , area of the exit of the aditus ad antrum to the mastoid antrum and connected mastoid air cells; A_{AD2} , area of the entrance to the aditus ad antrum from the middle ear cavity. For modeling purposes, we have calculated the radius (R_{AD1} and R_{AD2} ; not shown), which would correspond to a circle with the given area for the exit (A_{AD1}) and entrance (A_{AD2}). (C1) L_{EAC} , length of the EAC, measured from the most lateral extent of the tympanic groove (defined by P^4) to the spina suprameatum. In *Pan*, the spina suprameatum is replaced by the superior-most point of the porus acusticus externus. (C2) R_{TM1} , half of the measured greater diameter of the tympanic membrane, measured in P^3 ; R_{TM2} , half of the measured lesser diameter (perpendicular to R_{TM1}) of the tympanic membrane, measured in P^3 ; R_{EAC1} and R_{EAC2} , half of the measured diameters of the two major perpendicular axes (superoinferior and mediolateral) of the EAC measured at P^4 . (D) is based on the profiles of the malleus and incus from the temporal bone AT-1907 and the stapes from Cranium 5. L_M , functional length of the malleus, measured as the maximum length from the superior border of the lateral process to the inferior-most tip of the manubrium; L_I , functional length of the incus, measured from the lateral-most point along the articular facet to the lowest point along the long crus in the rotational axis; A_{FP} , measured area of the footplate of the stapes.

chimpanzees and humans, making it difficult to interpret the possible significance of interspecific differences. The tympanic membrane in the early hominins is reduced compared with that in chimpanzees and resembles that in humans in absolute size. The lever ratio of the auditory ossicles in the single early hominin individual in which this could be determined (*P. robustus*) is intermediate between the low value in humans and the higher value in chimpanzees. The additional data reported here have also confirmed the small size of the stapes footplate in early hominins, more closely resembling that in chimpanzees, and *A. africanus* shows a smaller stapes footplate than does *P. robustus*. Thus, compared with chimpanzees, the early hominin taxa are derived toward

modern humans in their slightly shorter and wider EAC, smaller tympanic membrane, and lower malleus/incus lever ratio but remain primitive in the small size of their stapes footplate. Although most of the relevant dimensions are similar between both early hominin taxa, *A. africanus* seems to be slightly smaller than *P. robustus* in the volume of the tympanic cavity and the sizes of the tympanic membrane and stapes footplate (Tables 1 and 2).

Auditory capacities

Some of these skeletal variables have a stronger influence on the sound power transmission results than others (Supplementary Materials; table S3).

Table 1. Measurements and summary statistics for the skeletal variables in chimpanzees and fossil and recent hominins.

Species	V_{MA}	V_{MEC}	L_{AD}	R_{AD1}	R_{AD2}	A_{TM}	$L_{EAC} (Com)$	A_{EAC}	L_M/L_I	A_{FP}	$M_M + M_I$	M_S
	Volume mastoid air cells cm^3	Volume tympanic cavity cm^3	Length of aditus mm	Radius of aditus exit mm	Radius of aditus entrance mm	Area of tympanic membrane mm^2	Complete length of external ear canal mm	Cross-sectional area of EAC mm^2	Malleus/ incus lever ratio	Area of stapes footplate mm^2	Mass of malleus + incus mg	Mass of stapes mg
<i>Homo sapiens</i> mean \pm SD	4.43 \pm 2.27	0.46 \pm 0.09	4.4 \pm 0.7	2.4 \pm 0.2	3.0 \pm 0.1	65.1 \pm 5.5	21.0 \pm 2.0	36.4 \pm 7.0	1.26 \pm 0.08	2.92 \pm 0.21	49.2 \pm 4.4	2.2 \pm 0.6
<i>Homo sapiens</i> range (n)	0.52–8.02 (10)	0.33–0.62 (10)	3.7–6.3 (10)	2.0–2.7 (10)	2.8–3.2 (10)	56.6–74.0 (10)	17.7–23.8 (10)	26.5–52.0 (10)	1.16–1.40 (7)	2.51–3.13 (7)	41.3–53.0 (8)	1.4–3.2 (8)
<i>Pan troglodytes</i> mean \pm SD	8.89 \pm 4.73	0.42 \pm 0.11	5.4 \pm 0.8	2.0 \pm 0.3	2.8 \pm 0.3	82.1 \pm 8.2	37.9 \pm 2.6	23.0 \pm 4.4	1.67 \pm 0.11	2.79 \pm 0.39	42.0 \pm 6.2	1.4 \pm 0.5
<i>Pan troglodytes</i> range (n)	2.25–18.73 (11)	0.26–0.62 (11)	3.6–6.8 (11)	1.5–2.4 (11)	2.3–3.3 (11)	71.0–102.8 (11)	34.2–40.8 (11)	16.4–30.3 (11)	1.52–1.79 (9)	2.40–3.48 (7)	35.0–53.0 (8)	1.0–2.2 (6)
Cranium 5	2.15	0.54	8.6	2.9	3.9	82.9	24.6	26.4		2.72		
AT-84						84.3	25.5	59.4		3.58		
AT-421						82.2	21.6	51.5		2.81		
AT-1907	3.68	0.76	5.2	3.1	3.9	74.8	24.0	30.2	1.19			
AT-4103	5.90	0.51	4.8	2.9	3.5	76.8	25.5	31.2				
Atapuerca (SH) mean \pm SD	3.91 \pm 1.89	0.60 \pm 0.14	6.2 \pm 2.1	3.0 \pm 0.1	3.8 \pm 0.2	80.2 \pm 4.2	24.2 \pm 1.6	39.7 \pm 14.7	1.19	3.04 \pm 0.47	52.7	
Atapuerca (SH) range (n)	2.15–5.90 (5)	0.51–0.76 (3)	4.8–8.6 (3)	2.9–3.1 (3)	3.5–3.9 (3)	74.8–84.3 (5)	21.6–25.5 (5)	26.4–59.4 (5)	(1)	2.72–3.58 (3)	(1)	
SK 46	2.55	0.43	6.1	1.8	2.7	62.3	27.2	47.6		2.44		
SK 47										2.61		
SK 52								40.7				
SK 848						69.8	30.0	47.2				
SK 879										2.43		
SKW 18	>3.92					67.0	29.8	38.8	1.36	2.42		
SKW 2581	>4.56						30.0	56.1				
SK 14003		0.53	4.4	1.9	2.8	63.3						
TM 1517						70.9	31.7	39.6				
<i>Paranthropus robustus</i> mean \pm SD	2.55	0.46 \pm 0.06	5.2	1.8	2.7	66.6 \pm 3.8	29.7 \pm 1.6	44.5 \pm 6.2	1.36	2.48 \pm 0.09		

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Species	V_{MA}	V_{MEC}	L_{AD}	R_{AD1}	R_{AD2}	A_{TM}	$L_{EAC} (Com)$	A_{EAC}	L_M/L_I	A_{FP}	$M_M + M_I$	M_S
	Volume mastoid air cells cm^3	Volume tympanic cavity cm^3	Length of aditus mm	Radius of aditus exit mm	Radius of aditus entrance mm	Area of tympanic membrane mm^2	Complete length of external ear canal mm	Cross-sectional area of EAC mm^2	Malleus/ incus lever ratio	Area of stapes footplate mm^2	Mass of malleus + incus mg	Mass of stapes mg
<i>Paranthropus robustus</i> range (n)	(1)	0.42–0.53 (3)	4.4–6.1 (2)	1.8–1.9 (2)	2.70–2.8 (2)	62.3–70.9 (5)	27.2–31.7 (5)	38.8–56.1 (7)	(1)	2.42–2.61 (4)		
STS 5						59.4	28.4					
STS 25		0.36			3.1	61.8	28.5	37.0				
STS 71							>27.8					
STW 98	3.43	0.23	4.7	1.1	2.1	57.3	27.4			2.31		
STW 151							>27.0	43.6		2.12		
STW 255										2.28		
STW 329	>1.19	0.31	5.6	1.8	2.5	65.1		39.5		1.87		
STW 370							>27.0					
STW 499						55.5		55.1				
STW 505							30.1					
<i>Australopithecus africanus</i> mean \pm SD	3.43	0.30 \pm 0.06	5.1	1.5	2.6 \pm 0.5	59.8 \pm 3.8	28.6 \pm 1.1	43.8 \pm 8.0		2.15 \pm 0.20		
<i>Australopithecus africanus</i> range (n)	(1)	0.23–0.36 (3)	4.7–5.6 (2)	1.1–1.8 (2)	2.1–3.1 (3)	55.5–65.1 (5)	27.4–30.1 (4)	37.0–55.1 (4)		1.87–2.31 (4)		

Generally, variables related with the EAC, tympanic membrane, and ear ossicles have a stronger influence on the model results, whereas the middle ear spaces (tympanic cavity, aditus ad antrum, and mastoid air cells) have a weaker influence. We have measured the sound power transmission values from 0 to 5.0 kHz and the occupied band (reflecting maximum sensitivity), defined by the frequency range (bandwidth), which concentrates more than 90% of the sound power that reaches the inner ear (see Materials and Methods), for all of the taxa.

The model results for chimpanzees and humans (Table 3, Fig. 2, and figs. S5 and S6) agree with published audiograms (3, 11, 12, 38). In particular, humans are characterized by a broad region of heightened sensitivity between about 1.0 and 4.5 kHz, whereas chimpanzees show a decrease in sensitivity above 3.0 kHz and reach a minimum between 4.0 and 5.0 kHz (Fig. 2). Between 1.0 and 5.0 kHz, the human mean sound power transmission values are significantly higher than in chimpanzees, except at 2.0 and 2.5 kHz (Tables 3 and 4). Similarly, the occupied band in humans is significantly wider (ca. 43%) than in chimpanzees and is shifted toward higher frequencies (Fig. 2).

The model results in both *A. africanus* and *P. robustus* are similar in the sound power transmission values and in the occupied band parameters (Table 3, Fig. 2, and fig. S7). Although the differences are somewhat larger above 4.0 kHz, this is primarily related to slight differences in the point of minimum sensitivity, with *P. robustus* showing a slightly lower frequency of minimum sensitivity (ca. 4.5 kHz) than *A. africanus* (>4.5 kHz). The occupied band is slightly wider (that is, larger bandwidth) in *A. africanus* than in *P. robustus*, but the SD of the pooled

early hominin sample is small compared with chimpanzees, suggesting that these minor differences in the early hominin taxa are likely not significant. These similarities suggest that the early hominin taxa have a shared pattern of sound power transmission and similar auditory capacities.

Regarding the sound power transmission values, the pooled early hominin sample is similar to chimpanzees up to 1.0 kHz, but more sensitive than chimpanzees from 1.5 to 3.5 kHz (Fig. 2 and Tables 3 and 4). The early hominins are also significantly different from and more sensitive than modern humans at all frequencies up to 3.0 kHz. Above 3.0 kHz, sensitivity begins to decrease in the early hominins, being similar to humans at 3.5 kHz and reaching a minimum between 4.5 and 5.0 kHz, resembling chimpanzees more closely. In addition, the occupied bandwidth in the pooled early hominins is similar to chimpanzees, but the occupied band itself is shifted toward slightly higher frequencies, as in humans (Fig. 2 and Tables 3 and 4). The occupied band is still narrower than in modern humans, but no difference was found in the lower limit of the bandwidth, suggesting that the differences reside mainly at the upper end. This shared pattern of sound power transmission in the early hominins can be distinguished from both chimpanzees and modern humans (Table 5).

Thus, between 1.5 and 3.0 kHz, the early hominins are more sensitive than either chimpanzees or modern humans. Above 3.5 kHz, the early hominins are less sensitive than modern humans, but similar to chimpanzees. The occupied band in the early hominins is similar to chimpanzees, but shifted toward higher frequencies at both the upper and lower ends. Further widening of the bandwidth in modern humans mainly involved higher frequencies toward the upper limit.

Table 2. Results of the Mann-Whitney *U* test for the anatomical variables. Values in bold indicate a significant difference ($P < 0.05$). Comparisons are limited to those variables with $n > 3$ for both taxa compared.

	Chimpanzees	<i>Australopithecus</i>	Chimpanzees	Chimpanzees	Modern humans	Modern humans
	versus	versus	versus	versus	versus	versus
Variable	modern humans	<i>Paranthropus</i>	<i>Australopithecus</i>	<i>Paranthropus</i>	<i>Australopithecus</i>	<i>Paranthropus</i>
V_{MA}	0.016	—	—	—	—	—
V_{MEC}	0.426	—	0.126	—	0.014	—
L_{AD}	0.010	—	—	—	—	—
R_{AD1}	0.003	—	—	—	—	—
R_{AD2}	0.043	—	0.456	—	0.287	—
A_{TM}	<0.001	0.032	<0.001	<0.001	0.075	0.679
L_{EAC}	<0.001	0.556	0.001	<0.001	0.002	0.001
A_{EAC}	<0.001	0.648	<0.001	<0.001	0.054	0.014
L_M/L_1	<0.001	—	—	—	—	—
A_{FP}	0.318	0.029	0.006	0.315	0.006	0.012
$M_M + M_I$	0.038	—	—	—	—	—
M_S	0.059	—	—	—	—	—

The middle Pleistocene Atapuerca (SH) hominins show a pattern of sound power transmission very close to that of modern humans (fig. S8). The Atapuerca (SH) hominins are significantly different from the pooled early hominins at all frequencies except 3.0 to 3.5 kHz and 5.0 kHz (Tables 3 and 4). Below 3.0 kHz, the early hominins are more sensitive than the Atapuerca (SH) hominins, whereas from 4.0 to 4.5 kHz, the Atapuerca (SH) hominins are more sensitive. The Atapuerca (SH) hominins show a significantly wider occupied band, which is shifted toward higher frequencies compared with the early hominins. Nevertheless, the lower limit of the bandwidth in the Atapuerca (SH) hominins is not significantly different from that of the pooled early hominins, indicating that the bandwidth was widened mainly at the upper end. Compared with modern humans, the occupied band in the Atapuerca (SH) hominins differs only in showing a slightly lower upper limit (Table 4).

DISCUSSION

The homogeneity in auditory capacities in both early hominin taxa is compatible with the similarity documented in most dimensions of their outer and middle ears (Table 1). In particular, the heightened sensitivity between 1.5 and 3.0 kHz in both early hominin taxa compared with chimpanzees and modern humans may be explained by variation in the skeletal structures that show a high influence on the model results in our analysis of sensitivity (table S3). These include the length (L_{EAC}) and cross-section (A_{EAC}) of the EAC, the size of the tympanic membrane (A_{TM}), and the lever ratio of the ear ossicles (L_M/L_1).

Although the human EAC is somewhat variable in shape, it is often modeled as a uniform tube that is closed at one end. The resonance frequency of such a tube is related to its length, and the corresponding

wavelength of the resonance frequency can be approximated as four times the length of the tube ($L_{EAC} \times 4$) (39, 40). This model of the EAC as a tube open at one end is valid for predicting resonance characteristics up to frequencies whose wavelengths are less than 10 times the smallest dimensions of the ear canal (39). In the early hominins, the mean L_{EAC} in *A. africanus* (28.6 mm) and *P. robustus* (29.7 mm) (Table 1) would correspond to resonance frequencies of about 3.0 and 2.9 kHz, respectively.

The narrower cross-sectional area of the EAC (A_{EAC}) in chimpanzees produces a higher surface area-to-volume ratio within the EAC. In mammals, higher ratios yield a higher impedance and less efficient transmission of sound to the tympanic membrane (30, 41). The values for the A_{EAC} in all the early hominin specimens fall above the chimpanzee and modern human means, indicating an absolutely wide EAC in both early hominin taxa (Table 1). Although the largest effects of the impedance on sound transmission in the EAC seem to be concentrated at frequencies <1.0 kHz (30, 41), differences in the impedance were noted at higher frequencies as well, and this may partially contribute to the greater sensitivity in early hominins between 1.5 and 3.0 kHz.

Regarding the tympanic membrane and ossicular lever ratio, the tympanic membrane in both early hominin taxa is close in size to that of humans (Table 1), whereas the ossicular lever ratio in *P. robustus* is somewhat higher. Thus, the tympanic membrane does not seem to be primarily driving the results. Although the lever ratio was found to be correlated mainly with low-frequency sensitivity (<1.0 kHz) across primates (42), the somewhat higher lever ratio in *P. robustus* (and, presumably, in *Australopithecus*) compared with humans may still provide an additional contribution to their heightened sensitivity between 1.0 and 3.0 kHz.

Regarding the upper and lower limits of the occupied band, the parameters that have more influence on the high and low cutoff frequencies

Table 3. Occupied band and sound power transmission values from 0.5 to 5.0 kHz. Negative values are in parentheses. Values in bold are means \pm SD.

		Occupied band			Sound power at the entrance to the cochlea (SPC)*									
		Lower limit	Upper limit	Bandwidth	SPC at 500 Hz	SPC at 1000 Hz	SPC at 1500 Hz	SPC at 2000 Hz	SPC at 2500 Hz	SPC at 3000 Hz	SPC at 3500 Hz	SPC at 4000 Hz	SPC at 4500 Hz	SPC at 5000 Hz
Species	n	(Hz)	(Hz)	(Hz)	(db)	(db)	(db)	(db)	(db)	(db)	(db)	(db)	(db)	(db)
<i>Australopithecus africanus</i> (STW 98)	1	760	3390	2630	3.1	13.7	9.1	11.1	13.5	14.6	7.0	-2.6	-13.3	-20.5
<i>Australopithecus africanus</i> (STS 25)	1	715	3310	2630	3.3	14.5	9.1	11.2	12.6	11.2	6.7	0.7	-5.4	-12.3
<i>Paranthropus robustus</i>	1	830	3410	2580	2.2	13.4	9.6	11.7	13.9	14.4	8.0	-2.4	-16.9	-6.5
Pooled early hominins mean \pm SD	3	768 \pm 58	3370 \pm 53	2602 \pm 26	2.9 \pm 0.6	13.9 \pm 0.6	9.3 \pm 0.3	11.3 \pm 0.4	13.3 \pm 0.7	13.4 \pm 1.9	7.2 \pm 0.7	(-1.4) \pm 1.9	(-11.8) \pm 5.9	(-13.1) \pm 7.0
Pooled early hominins range		715-830	3310-3410	2580-2630	2.2-3.3	13.4-14.5	9.1-9.6	11.1-11.7	12.6-13.9	11.2-14.6	6.7-8.0	(-2.6)-0.7	(-16.9)-(-5.4)	(-20.5)-(-6.5)
<i>Pan troglodytes</i> mean \pm SD	11	570 \pm 54	3015 \pm 122	2445 \pm 134	3.8 \pm 1.2	12.9 \pm 1.3	7.1 \pm 0.8	8.4 \pm 1.1	8.2 \pm 1.6	5.9 \pm 1.3	0.2 \pm 2.6	(-7.0) \pm 4.8	(-10.5) \pm 5.3	(-10.7) \pm 6.1
<i>Pan troglodytes</i> range		490-650	2750-3205	2185-2635	1.6-5.8	10.5-14.4	5.8-8.9	6.9-10.1	5.9-11.2	3.2-7.4	(-3.2)-3.6	(-16.6)-(-2.2)	(-22.7)-(-3.6)	(-17.5)-(-0.6)
Atapuerca (SH) mean \pm SD	5	791 \pm 93	3969 \pm 166	3178 \pm 213	0.8 \pm 0.9	11.7 \pm 1.2	7.9 \pm 0.2	9.0 \pm 0.8	8.8 \pm 1.8	8.6 \pm 2.9	8.3 \pm 2.5	6.4 \pm 2.0	1.1 \pm 1.6	(-5.2) \pm 2.2
Atapuerca (SH) range		715-930	3760-4155	2830-3365	(-0.2)-1.9	9.7-13.0	7.6-8.0	7.9-10.2	6.5-11.5	5.3-12.9	5.3-11.1	4.8-9.8	(-1.1)-2.8	(-8.5)-(-3.0)
<i>Homo sapiens</i> mean \pm SD	10	841 \pm 95	4339 \pm 332	3498 \pm 349	0.8 \pm 1.7	10.3 \pm 1.8	8.0 \pm 0.4	9.0 \pm 0.7	9.1 \pm 1.1	8.7 \pm 1.5	8.5 \pm 1.8	8.0 \pm 1.8	5.1 \pm 3.2	(-0.9) \pm 5.2
<i>Homo sapiens</i> range		720-1065	3870-4950	3035-4230	(-3.8)-2.1	5.5-11.8	7.4-8.5	7.8-9.9	6.9-10.5	5.7-10.4	4.9-10.5	5.3-10.4	(-1.2)-10.7	(-11.5)-4.6

*Sound power at the entrance to the cochlea relative to $P_0 = 10^{-18}$ W for an incident plane wave intensity of 10^{-12} W/m².

are the length (L_{EAC}) and cross-sectional area (A_{EAC}) of the ear canal, the area of the tympanic membrane (A_{TM}), the volumes of the middle ear cavities (V_{MA} and V_{MEC}), and the length (L_{AD}) and radii (R_{AD1} and R_{AD2}) of the aditus ad antrum. The resonance frequency of the ear canal, which is dependent on its length, is directly related to both cutoff frequencies. When the ear canal is narrower, as in chimpanzees, the power at the input is lower at intermediate frequencies, mainly in the range from 2 to 4 kHz. In addition, a larger tympanic membrane, as in chimpanzees, produces higher input impedance and higher losses in sensitivity, especially for frequencies above 1 kHz. The middle ear cavities produce a notch (loss in sound power transmission), which is related with the volume of the middle ear cavities and the dimensions of the aditus ad antrum (figs. S9 to 12). The lower the frequency of the notch, the lower the high cutoff frequency for the occupied band.

The shorter EAC length in the early hominins, compared with chimpanzees, likely reflects the mediolateral expansion of the central basicranium and a reduction of the tympanic length in early hominins associated with the forward migration of the foramen magnum (43-45), likely related to the adoption of habitual upright posture. In addition, the size re-

duction of the tympanic membrane and the changes in the malleus proportions (26) might plausibly be explained as pleiotropic effects of these changes in the EAC. This hypothesis finds some support in the strong developmental integration of the EAC and the tympanic membrane and malleus manubrium (46, 47). Perhaps relevant in this regard, a recent study has documented morphological integration between the cranial base and the inner ear in modern humans, with changes in cranial base width affecting certain dimensions of the bony labyrinth (48). The auditory consequences of these anatomical changes in the early hominins are a greater sensitivity from 1.5 to 3.5 kHz, compared with chimpanzees. Indeed, the early hominins are more sensitive than both chimpanzees and humans from 1.5 to 3.0 kHz.

The present results make it possible to outline the evolutionary transformation of the human audiogram, and suggest two main stages in the evolution of hominin audition. Compared with chimpanzees, early hominins show a greater sensitivity between 1.5 and 3.5 kHz and an occupied band that is shifted toward slightly higher frequencies. In both these aspects, the early hominins are derived compared with chimpanzees. Subsequently, the genus *Homo* experienced a considerable

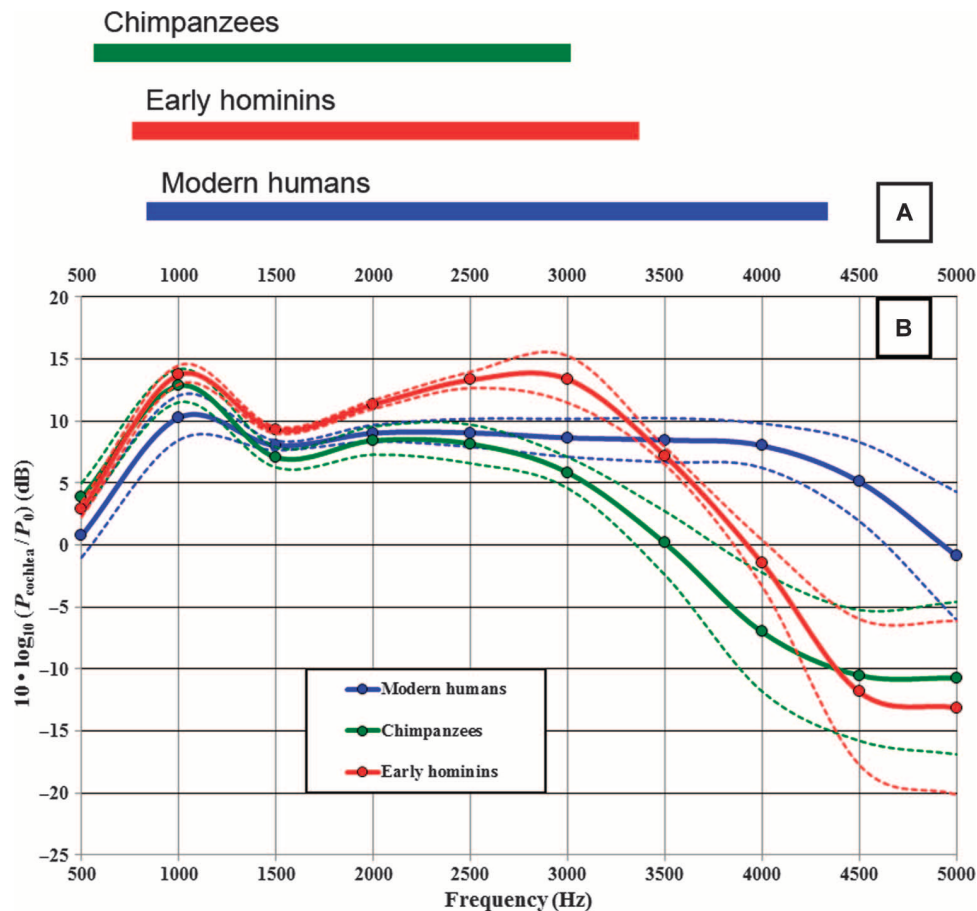


Fig. 2. Model results for chimpanzees, modern humans, and early hominins from 0.5 to 5.0 kHz. (A) The occupied band is similar in chimpanzees and early hominins, but is shifted toward slightly higher frequencies in the latter. Modern humans show a widened occupied band that is further extended toward higher frequencies. **(B)** The sound power transmission curves correspond to decibels at the entrance to the cochlea relative to $P_0 = 10^{-18}$ W for an incident plane wave intensity of 10^{-12} W/m². The mean value ± 1.0 SD for each frequency position is shown for each group. Points higher along the curve indicate better sound power transmission and heightened auditory sensitivity. Individual results are provided in figs. S5 to S8.

widening of the occupied band, which is extended toward higher frequencies (>3.5 kHz) (Fig. 2). This widened occupied band was already largely present by at least the Middle Pleistocene, because it has been identified in the Atapuerca (SH) hominins.

In modern humans, it is reasonable to suggest that this wider occupied band extended toward higher frequencies facilitated the specialization of our species in the use of complex short-range vocal communication. In particular, high-frequency consonants (for example, those associated with the phonemes t, k, f, and s) have a considerable amount of energy concentrated within the frequency range from 3 to 5 kHz (49) and are particularly salient features of human spoken language (50). Indeed, the use of consonants is one of the main distinctions, along with a symbolic component, between human language and most forms of animal communication (51).

In contrast, it has been suggested that communication in early hominins was likely largely restricted to a vowel-based system (52, 53). However, many high-frequency consonants are voiceless consonants, and their production is not dependent on the resonance properties of the vocal tract but is more strongly determined by articulations between the teeth, lips, palate, and tongue. In addition, they are among the easiest consonants to produce in terms of articulatory complexity (54). Such

voiceless consonants are useful only in short-range communication, and this emphasis on consonant production is consistent with the “general perspective that speech evolved through imposing articulatory gestures on a vowel-based carrier signal” [(52, 53), p. 1736]. Although the precise nature of early hominin communication remains elusive, it may have involved some form of “low-fidelity social transmission” beyond that of a chimpanzee (55). Such communication need not have contained a symbolic component.

Perhaps more relevant to the present results, studies of habitat acoustics have suggested that the structural properties of primate vocalizations are related to environmental characteristics (56, 57). Lower-frequency calls, generally ≤ 1 kHz, emitted by arboreal primates travel far in the rainforest canopy and are important for maintaining intergroup spacing. However, attenuation of the sound signal at distances ≥ 25 m is considerably greater in open environments, such as the savanna, and the presence of the visual channel further limits the use of long-range intergroup calls by terrestrial primates (57). In contrast, short-range communication (generally ≤ 25 m) is more strongly dependent on ambient background noise, which is lower across most frequencies up to 10 kHz in the savanna. This combination of higher signal attenuation and lower ambient background noise means that short-range intragroup communication

Table 4. Mann-Whitney *U* test results for the occupied band and sound power transmission values from 0.5 to 5.0 kHz. Values in bold indicate a significant difference ($P < 0.05$).

	Chimpanzees versus modern humans	Early hominins versus chimpanzees	Early hominins versus modern humans	Early hominins versus Atapuerca (SH)	Atapuerca (SH) versus modern humans
Band lower limit	<0.001	0.005	0.217	0.786	0.371
Band upper limit	<0.001	0.005	0.007	0.036	0.028
Bandwidth	<0.001	0.126	0.007	0.036	0.075
SPC at 500 Hz	<0.001	0.126	0.007	0.036	0.594
SPC at 1000 Hz	<0.001	0.225	0.007	0.036	0.075
SPC at 1500 Hz	0.003	0.005	0.007	0.036	0.254
SPC at 2000 Hz	0.282	0.005	0.007	0.036	0.953
SPC at 2500 Hz	0.251	0.005	0.007	0.036	0.679
SPC at 3000 Hz	0.001	0.005	0.007	0.071	0.679
SPC at 3500 Hz	<0.001	0.005	0.217	0.786	0.953
SPC at 4000 Hz	<0.001	0.088	0.007	0.036	0.165
SPC at 4500 Hz	<0.001	0.769	0.007	0.036	0.013
SPC at 5000 Hz	0.001	0.769	0.014	0.071	0.075

Table 5. Results of the discriminant function analysis for the sound power transmission values.

	% Correct classification*	<i>Homo sapiens</i>	<i>Pan troglodytes</i>	Early hominins	Total
<i>Homo sapiens</i>	100.0	10	0	0	10
<i>Pan troglodytes</i>	100.0	0	11	0	11
Early hominins	100.0	0	0	3	3
Total	100.0	10	11	3	24

*All specimens were classified with very high posterior probabilities (>0.99).

is favored in open habitats, and the fine structure of the signal acoustics may be expected to be more elaborate and varied (57). This relationship has been used for the vervet monkey (*Chlorocebus aethiops*), a species that regularly occupies open habitats, to explain both their vocal repertoire, which includes short-range sounds, some of which reach up to 5 kHz (58), and shows complex acoustic features (59), and their auditory pattern, which shows a heightened sensitivity to frequencies between 1 and 8 kHz (3, 60). Both *A. africanus* and *P. robustus* are reported to have regularly consumed open habitat resources, perhaps constituting up to 50% of their diet (61, 62). Thus, the early hominin auditory pattern may have facilitated and reinforced an increased emphasis on short-range vocal communication in open habitats.

MATERIALS AND METHODS

Study design

Sample size and measurements. We have relied mainly on CT scans and virtual reconstructions of the outer and middle ear using the

Mimics (Materialise) software package to measure a series of linear, areal, and volumetric variables in the early hominin specimens SK 46 (*P. robustus*), STW 98 (*A. africanus*), and STS 25 (*A. africanus*), as well as samples of *P. troglodytes* ($n = 11$) and *Homo sapiens* ($n = 10$) (see Fig. 1 and the Supplementary Materials). Data from a number of less complete early hominin specimens were also collected relying on either virtual reconstructions or direct measurements on the original fossils when the outer or middle ear was exposed and accessible (see the Supplementary Materials). Data on the Middle Pleistocene Atapuerca (SH) hominins were taken from previous publications (14, 15).

For the auditory ossicles, we relied on measurements taken on scaled digital images of the malleus, incus, and stapes in standardized orientations once they were removed from the tympanic cavity (26, 63, 64). When the stapes is not preserved, we relied on measurements taken on scaled digital images of the oval window area in those specimens where it could be directly observed and photographed. We applied a 90% correction factor to the oval window area to account for the size of the annular ligament (64).

The auditory capacities were modeled only in those early hominin specimens where most of the relevant dimensions could be measured.

Nevertheless, the variable preservation of the fossils means that inevitably some dimensions were not preserved. Thus, a few dimensions were estimated on the basis of the species mean values. We are also aware of the difficulties with taxonomic assignments for many of the early hominin specimens, particularly from Sterkfontein [see (65) for a recent review].

Modeling auditory capacities. We have relied on a slightly modified version of the model published by Rosowski (30) to estimate the sound power transmission through the outer and middle ear (see the Supplementary Materials and fig. S4). The electrical parameters used in the model are associated with anatomical structures of the ear. Some of these parameters are related with skeletal structures accessible in fossils, whereas others are related with soft tissues that are not preserved in fossil specimens. We have measured or accurately estimated in the fossil specimens and comparative samples all of the skeletal variables included in the model (Table 1 and table S3). For the soft tissue variables that cannot be measured in dried skulls (that is, chimpanzees and recent humans) or fossil specimens, we have used the values for modern humans (30, 66) for all taxa in the present study. Notably, only seven of these have an appreciable effect on the model results above 2 kHz (labeled as medium and high in table S3).

We performed an analysis of the sensitivity of the model to determine the influence of the individual variables on the model results above 2 kHz (table S3). Sensitivity is related to the difference in the value for sound power at the entrance to the cochlea (in decibels) obtained by increasing and decreasing the individual anatomical variable or electrical parameter by 50%. Sensitivity has been classified into three broad groupings: low (≤ 1 dB difference), medium (>1 to ≤ 3 dB difference), and high (>3 dB difference). In general, variables of the outer ear and ear ossicles have a stronger influence on the model results, whereas the middle ear spaces (tympanic cavity, mastoid antrum and air cells, and aditus ad antrum) have a weaker influence on the results.

The model results for the sound power transmission through the outer and middle ear were used to estimate the frequency band of maximum sensitivity, as well as the resulting bandwidth and its upper and lower cutoff frequencies. Although a number of definitions can be considered, the occupied band (67) is defined by the bandwidth such that under the lower cutoff frequency and above the upper cutoff frequency, the average power is equal to a specified percentage, $b/2$, of the total average power. Here, $b/2$ is considered as equal to 5%, such that the occupied bandwidth includes the range of frequencies that contains at least 90% of the sound power transmitted to the inner ear for an incident plane wave with flat spectrum.

Statistical analysis

Given the small sample sizes involved in the present study, we have relied on the Mann-Whitney U test to examine statistical differences in the anatomical variables and auditory capacities between groups. Significance was determined relying on the exact P value ($P < 0.05$), given the small sample sizes. Subsequently, discriminant function analysis was performed on the sound power transmission values between 0.5 and 5.0 kHz for all the extant and fossil taxa. The prior probabilities for group membership for any given specimen were determined to be equal, because the differences in sample size do not reflect true differences in population size between the taxa under consideration (68). All statistical analyses were performed using the Statistica software program.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/1/8/e1500355/DC1>

Comparative sample composition

Preservation of early hominin specimens

CT scanning of modern human, chimpanzee, and fossil hominin specimens

Model description

Comparison of present measurements with previous studies

Fig. S1. Virtual (3D CT) reconstruction of the outer, middle, and inner ears in *P. robustus* (SK 46).

Fig. S2. Model results for the effects of intraindividual measurement error on the sound power transmission in two reconstructions of the CSJ 26 *H. sapiens* individual.

Fig. S3. Model results for the effects of interindividual measurement error on the sound power transmission in two reconstructions of the HTB 3434 *P. troglodytes* individual.

Fig. S4. Block diagram of the analog electrical circuit model based on (30).

Fig. S5. Model results for sound power transmission in chimpanzees.

Fig. S6. Model results for sound power transmission in modern humans.

Fig. S7. Model results for sound power transmission in the early hominins.

Fig. S8. Model results for sound power transmission in the Middle Pleistocene Atapuerca (SH).

Fig. S9. Model results for the magnitude of the middle ear gain (|GME|) in modern humans.

Fig. S10. Model results for the magnitude of the middle ear gain (|GME|) in chimpanzees.

Fig. S11. Model results for the magnitude of the middle ear gain (|GME|) in early hominins.

Fig. S12. Model results for the magnitude of the middle ear gain (|GME|) in the Atapuerca (SH) specimens.

Table S1. Measurements and model results for the influence of intraindividual measurement error.

Table S2. Measurements and model results for the influence of interindividual measurement error.

Table S3. Definition of the electrical parameters, their related anatomical variables, the source of the value used, and the sensitivity analysis for frequencies above 2 kHz in the model.

Table S4. Measurements in the present study compared with those reported previously.

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