

Document downloaded from the institutional repository of the University of Alcalá: <https://ebuah.uah.es/dspace/>

This is an Accepted Manuscript version of the following article, accepted for publication in *Nature ecology & evolution*:

Conde-Valverde, M. *et al.* (2021) 'Neanderthals and Homo sapiens had similar auditory and speech capacities', *Nature ecology & evolution*, 5(5), pp. 609–615. [doi:10.1038/s41559-021-01391-6](https://doi.org/10.1038/s41559-021-01391-6)

It is deposited under the terms of the Creative Commons Attribution-Non-Commercial-NoDerivatives License:

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way.

<https://www.springernature.com/gp/open-research/policies/accepted-manuscript-terms>



This work is licensed under a  
Creative Commons Attribution-NonCommercial-NoDerivatives  
4.0 International License.

*(Article begins on next page)*



# Universidad de Alcalá



This work is licensed under a  
Creative Commons Attribution-NonCommercial-NoDerivatives  
4.0 International License.

1 **Title: Neanderthals and *Homo sapiens* had similar auditory and speech capacities**

2 **Authors:** Mercedes Conde-Valverde<sup>1\*</sup>, Ignacio Martínez<sup>1,2</sup>, Rolf M. Quam<sup>1,2,3,4</sup>, Manuel Rosa<sup>1,5</sup>,  
3 Alex D. Velez<sup>3</sup>, Carlos Lorenzo<sup>6,7</sup>, Pilar Jarabo<sup>5</sup>, José María Bermúdez de Castro<sup>8,9</sup>, Eudald  
4 Carbonell<sup>6,7,10</sup>, Juan Luis Arsuaga<sup>2,11</sup>

5 **Affiliations:**

6 <sup>1</sup>Cátedra de Otoacústica Evolutiva y Paleoantropología (HM Hospitales-Universidad de Alcalá),  
7 Departamento de Ciencias de la Vida, Universidad de Alcalá, Campus Universitario, Ctra.  
8 Madrid-Barcelona Km 33,600. 28871 Alcalá de Henares, Madrid, Spain.

9 <sup>2</sup>Centro Mixto (UCM-ISCIII) de Evolución y Comportamiento Humanos, Av. Monforte de Lemos  
10 5, 28029 Madrid, Spain.

11 <sup>3</sup>Department of Anthropology, Binghamton University (SUNY) Binghamton, NY 13902-6000  
12 USA.

13 <sup>4</sup>Division of Anthropology, American Museum of Natural History, Central Park West-79th St.,  
14 New York, NY 10024, USA.

15 <sup>5</sup>Departamento de Teoría de la Señal y Comunicaciones, Escuela Politécnica Superior,  
16 Universidad de Alcalá, Campus Universitario, 28805 Alcalá de Henares, Spain.

17 <sup>6</sup>Àrea de Prehistòria, Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Av.  
18 Catalunya 35, 43002 Tarragona, Spain.

19 <sup>7</sup>Institut Català de Paleoecologia Humana i Evolució Social, Campus Sescelades URV, Zona  
20 Educacional 4, 43007 Tarragona, Spain.

21 <sup>8</sup>Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Burgos, Spain.

22 <sup>9</sup>Anthropology Department, University College London, London, UK.

23 <sup>10</sup>Departamento de Historia, Geografía y Comunicación, Universidad de Burgos, Paseo de los  
24 Comendadores s/n, 09001 Burgos, Spain

25 <sup>11</sup>Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias  
26 Geológicas, Universidad Complutense de Madrid, 28040 Madrid, Spain

27 \*Correspondence to: mercedes.conde@fgua.es.  
28

29 **Abstract: The study of audition in fossil hominins is of great interest given its**  
30 **relationship with intraspecific vocal communication. While the auditory capacities have**  
31 **been studied in early hominins and in the Middle Pleistocene Sima de los Huesos (SH)**  
32 **hominins, less is known about the hearing abilities of the Neanderthals. Here we provide**  
33 **a detailed approach to their auditory capacities. Relying on CT scans and a**  
34 **comprehensive model from the field of auditory bioengineering, we have established**  
35 **sound power transmission through the outer and middle ear and calculated the occupied**

36 **bandwidth in Neanderthals. The occupied bandwidth is directly related to the efficiency**  
37 **of the vocal communication system of a species. Our results show that the occupied**  
38 **bandwidth of Neanderthals was greater than the SH hominins and similar to extant**  
39 **humans, implying that Neanderthals had evolved the auditory capacities to support a**  
40 **vocal communication system as efficient as modern human speech.**

## 41 **Introduction**

43 The linguistic capacities in Neanderthals have long been an area of active research and debate  
44 among paleoanthropologists, albeit with little resolution<sup>1-3</sup>. The last two decades have seen  
45 increasing archaeological discoveries documenting complex behaviors in Neanderthals. These  
46 have been linked to the possible presence of language in Neanderthals, since it seems  
47 reasonable to suggest that such behaviors require the presence of a complex and efficient oral  
48 communication system<sup>3</sup>. Nevertheless, a different point of view maintains that the distinctive  
49 features of human language, absent in other organisms, include a symbolic element as well as  
50 a recursive syntactic process called “merge”<sup>4</sup>. This latter process, at its simplest, uses two  
51 syntactic elements and assembles them to form a set and is argued to be exclusive to *Homo*  
52 *sapiens* and to have appeared no earlier than 100 ky<sup>1,4</sup>.

53 Tracing the presence of symbolism and syntactic processes in the course of human  
54 evolution currently lies outside the realm of possibility in paleontology<sup>1</sup>. Nevertheless, the study  
55 of human fossils can prove key to determining whether past human species, and in particular  
56 the Neanderthals, possessed the anatomy necessary to produce and perceive an oral  
57 communication system as complex and efficient as human speech, the usual (but not exclusive)  
58 vehicle for language. In other words, although paleontology cannot study the evolution of the  
59 “software” of language it can contribute to our understanding of the evolution of the “hardware”  
60 of speech. In our opinion, to suggest that a past human species, such as the Neanderthals, may  
61 have had language, it is not only necessary to establish the presence of symbolism, which can

62 be approached in the archaeological record<sup>1</sup>, but also to demonstrate the existence of the  
63 anatomical bases necessary to produce and perceive articulated speech.

64 The study of brain endocasts has been one of the classic approaches to interpreting the  
65 cognitive and linguistic capacities in Neanderthals. Although the Neanderthals as a species are  
66 as encephalized as *H. sapiens*<sup>5,6</sup>, clear differences have been documented in the cerebral  
67 organization<sup>7-9</sup> as well as the allometric trajectories in both phylogenetic<sup>10</sup> and ontogenetic<sup>11</sup>  
68 terms. Nevertheless, the significance of these differences for inferring cognitive and linguistic  
69 capacities in Neanderthals remains actively debated<sup>2,4,8,9,12,13</sup>.

70 During the last five decades, much debate has centered on whether the supralaryngeal  
71 vocal tract in Neanderthals was capable of producing the fundamental sounds of human  
72 speech<sup>2</sup>. While this debate remains unresolved, recent anatomical<sup>14-16</sup> and genetic<sup>17</sup> data  
73 support the idea that Neanderthals could have produced a wide repertoire of acoustic signals,  
74 facilitating a complex form of vocal communication. In this context, it would be particularly  
75 interesting to establish whether the auditory capacities in Neanderthals were capable, or not, of  
76 supporting a vocal communication system as efficient as that of our own species.

77 The auditory capacities in Neanderthals have been indirectly approached through  
78 comparative studies of the dimensions and proportions of the ear ossicles<sup>18</sup> as well as the  
79 functional properties of the middle ear<sup>19</sup>. These studies found broad similarities between  
80 Neanderthals and modern humans in both aspects, suggesting that these similarities might  
81 imply similar hearing abilities as well. On the other hand, based on a few features of the external  
82 and middle ear, Masali<sup>20</sup> proposed that Neanderthals had a slightly higher best audible  
83 frequency than modern humans.

84 More recently, a comprehensive model, based on a large number of anatomical  
85 variables directly related to auditory physiology, has been used to estimate the sound power  
86 transmission (SPT) through the outer and middle ear in fossil hominins<sup>14,21-22</sup>. The SPT reflects  
87 the acoustic filtering process, leading to a frequency-dependent attenuation of sound power at

88 the cochlear entrance, which largely shapes the resultant audiogram in living subjects<sup>23</sup>. The  
89 SPT directly depends on the dimensions of the different anatomical structures of the outer and  
90 middle ear<sup>23</sup>, making it possible to estimate it in fossil species.

91 At the same time, based on the SPT it is also possible to calculate the occupied bandwidth  
92 (OBW), defined as the width of a frequency band such that, below the lower and above the  
93 upper frequency limits, the mean powers are each equal to a specified percentage of the total  
94 mean power of a given signal spectrum<sup>24</sup>. In the present study, the OBW includes the range of  
95 frequencies which contains at least 90% of the sound power transmitted to the inner ear<sup>14,21,22</sup>,  
96 reflecting the frequency range of maximum auditory sensitivity. The OBW is, in turn, directly  
97 related to the bandwidth of the oral communication channel. A wider communication channel  
98 bandwidth allows for a larger number of easily distinguishable acoustic signals to be used in the  
99 oral communication of a species. This improves the efficiency of communication (i.e. the ability  
100 to deliver a clear message in the shortest amount of time) since it allows for an increase in the  
101 number of phonemes and a reduction of the perception error rate<sup>25</sup>.

102 The theory of information, as outlined by Shannon<sup>25</sup>, has been used to estimate the information  
103 rate of speech communication<sup>26</sup>, and forms the basis for recent studies examining the  
104 correlation between speech intelligibility and bandwidth for normal and hearing impaired  
105 people<sup>27,28</sup>. The influence of bandwidth reduction on speech intelligibility is reflected in the  
106 definition of the ANSI/ASA S3.5-1997 speech intelligibility index standard<sup>29,30</sup>. Thus, there is a  
107 clear link between the OBW and the oral communication system in humans.

108 Previous studies carried out on the European middle Pleistocene fossils from the Sima  
109 de los Huesos (SH)<sup>14,22</sup> and in the early hominin taxa *Australopithecus africanus* and  
110 *Paranthropus robustus* from South Africa<sup>21</sup> showed that the OBW in the early hominins was  
111 quite similar to *Pan troglodytes*, while the SH fossils had an OBW more similar to, although  
112 somewhat narrower than, *H. sapiens*. In this context, establishing the OBW in Neanderthals

113 would be particularly interesting. If this parameter is similar to that in the SH hominins, it could  
114 be argued that the Neanderthals developed more complex behaviors than their ancestors  
115 without the need to increase the efficiency of their communication system. Nevertheless, if the  
116 OBW in Neanderthals is wider than in the SH hominins, this would show that the increased  
117 behavioral complexity of the Neanderthals, compared with their ancestors, was accompanied by  
118 an increase in the efficiency of the oral communication system, suggesting a functional link  
119 between these two phenomena.

120 To establish the SPT and OBW in Neanderthals, we virtually reconstructed the outer and  
121 middle ears in five Neanderthal individuals (Fig. 1) from CT scans. We have also reconstructed  
122 the outer and middle ears in six new SH individuals and have carried out new reconstructions of  
123 three previously published individuals<sup>14,21,22</sup> based on higher resolution CT scans (Extended  
124 Data 1). These new data on the SH hominins are particularly relevant given their close  
125 phylogenetic relationship between the SH population and Neanderthals<sup>5,31</sup>. The fossil samples  
126 were compared with a sample of recent *H. sapiens* (n = 10) published previously<sup>21</sup>.  
127 Based on anatomical measurements taken on the 3D models (Extended Data 2; Supplementary  
128 Table 1), we have calculated the SPT and OBW in the Neanderthals and the expanded SH  
129 sample (Table 1, Figs. 2, 3; Extended Data 3; Supplementary Table 2).

130

## 131 **Results**

### 132 Comparison with previous studies of the Sima de los Huesos fossils

133 The auditory capacities in the SH fossils have been studied previously<sup>14,22,32</sup>. However, the SH  
134 sample used in the present study includes novel data in several regards. First, the present study  
135 only includes complete individuals, where all the measurements of the outer and middle ear can  
136 be taken. Thus, two previously published incomplete individuals (AT-84 and AT-421), which  
137 relied on estimating the values for some missing variables<sup>22</sup>, have been removed from the  
138 sample. In addition, previous studies on the auditory capacities of the SH hominins used

139 medical CT scans for Cr. 3, Cr. 5 and AT-1907<sup>22</sup>. These same three individuals have now been  
140 CT scanned at a higher resolution, along with all the new SH individuals included in this study  
141 (Cr.4, Cr.7, Cr.8, Cr.13, Cr.15, Cr.16) (Supplementary Table 3). As a consequence, we carried  
142 out new reconstructions of the external and middle ear cavities of Cr.3, Cr.5 and AT-1907, using  
143 the new CT scans and obtained new values for the anatomical variables (Supplementary Table  
144 1). The descriptive statistics of the anatomical variables and the SPT in 7 SH individuals, relying  
145 on the new reconstructions, were published previously<sup>32</sup>, but here we include for the first time  
146 the individual values for these variables in these same individuals, together with the unpublished  
147 values in Cr.16 (Supplementary Table 1 for anatomical variables and Supplementary Table 2 for  
148 SPT values). In addition, we provide here for the first time the individual values for the OBW, a  
149 central objective of the present study, for all the SH individuals based on the higher resolution  
150 CT scans (Supplementary Table 2).

151 For Cr.3 and AT-1907, the differences between the previous anatomical measurements and the  
152 new values are very small (Supplementary Table 1), and the differences for SPT and OBW are  
153 also very small (Extended Data 4). In the case of Cr.5, the differences between the previously  
154 published values and the new data are greater, particularly for the variables  $L_{AD}$ ,  $A_{TM}$ ,  $L_{EAC}$  and  
155  $A_{EAC}$ , and the SPT and OBW have also been affected. In particular, the OBW in Cr.5 is narrower  
156 than previously published (Extended Data 4), although, importantly, the new value for OBW falls  
157 within the range of variation in the expanded SH sample.

158 The mean value for OBW in the enlarged SH sample is slightly lower than that previously  
159 published<sup>22</sup>. The new SH mean is still significantly higher than the mean OBW in *P. troglodytes*  
160 (Extended Data 5) but is significantly lower than that in modern humans (Table 1). This lower  
161 mean value is mainly due to the low values for OBW obtained in three new individuals included  
162 in this study: Cr.4, Cr.8 and Cr.13 (Supplementary Table 2). These are the three largest crania  
163 in the SH sample, based on their cranial capacities (Supplementary Table 4). This relationship  
164 between cranial size and OBW is explained by the fact that the largest crania also tend to show



165 the longest external auditory canals. Since the length of the external auditory canal is strongly  
166 negatively correlated with the OBW (Extended Data 6), the inclusion of the largest crania in the  
167 sample has lowered the mean OBW for the SH hominins. Given this relationship between  
168 cranial size and the OBW, it is important to emphasize that our Neanderthal comparative  
169 sample includes the smallest (La Quina H5) as well as two of the largest (La Chapelle-aux-  
170 Saints 1, Amud 1) known Neanderthal crania (Supplementary Table 2).

### 171 Results in the Neanderthals

172 The results revealed no statistically significant differences between the Neanderthal and modern  
173 human means in any of the anatomical variables (Extended Data 7), nor the SPT (Fig. 2;  
174 Extended Data 3) or OBW (Table 1, Fig. 3). Contrary to previous suggestions<sup>20</sup>, our results for  
175 the SPT indicate a similar best frequency in Neanderthals and modern humans. More  
176 importantly, the OBW values for Neanderthals fall within the modern human range of variation,  
177 except for La Chapelle-aux-Saints1, which is just below the lower limit of modern humans. At  
178 the same time, Neanderthals show some differences from the SH sample in a few anatomical  
179 variables (Extended Data 7), as well as the SPT at frequencies between 4-5 kHz (Fig. 2;  
180 Extended Data 3) and the OBW, which is wider in Neanderthals (Table 1, Fig. 3) and extended  
181 towards higher frequencies. These differences in the OBW can be explained by the significantly  
182 lower values in Neanderthals than in the SH sample for a few anatomical variables, including  
183 the volume of the *aditus* ( $V_{AD}$ ), radius of the entrance of the *aditus* ( $R_{AD(entrance)}$ ) and length of the  
184 external auditory canal ( $L_{EAC}$ ), which show negative correlations (especially  $L_{EAC}$ ) with the OBW  
185 (Extended Data 6).

### 186 **Discussion and Conclusions**

187  
188 Our results show that the auditory capacities in Neanderthals do not differ from those in  
189 modern humans, including the presence of an extended OBW in both species. Importantly, the  
190

191 OBW in Neanderthals extends towards frequencies which primarily involve consonant  
192 production<sup>33</sup>, suggesting this may have been a significant component of their vocal  
193 communication, one which would distinguish them from the pattern of largely vowel-based vocal  
194 communication in chimpanzees<sup>34</sup> and, indeed, nearly all mammals<sup>35</sup>. Although much of the  
195 acoustic information in human speech is concentrated in the region up to around 2.5 kHz (e.g.,  
196 the first two formant frequencies of the vowels), the region between 3-5 kHz is associated with  
197 the production of high frequency consonants<sup>33</sup>. Consonants in this frequency range mainly  
198 consist of the voiceless plosives (stops), such as those associated with the sounds  
199 corresponding to the English letters /t/ and /k/, and the voiceless fricatives including those  
200 associated with the sounds corresponding to the English letters /f/, /s/ and /th/. While other  
201 consonants do occur at lower frequencies, the high frequency consonants are particularly  
202 salient features in human speech. Voiceless plosives are present in over 90% of the world's  
203 languages, with /t/ and /k/ being the most strongly represented<sup>36</sup>. Similarly, fricative consonants  
204 are found in more than 90% of the world's languages, and among the fricatives, /s/ is the most  
205 common voiceless fricative, present in over 80% of languages, with /f/ also occurring at high  
206 frequencies<sup>36</sup>. Importantly, because these consonants are voiceless, they do not propagate  
207 across the landscape and are limited to short-range intraspecific communication. Indeed,  
208 voiceless consonants may represent "...the evolutionarily oldest group of consonants"<sup>37</sup>.

209 In addition, there is evidence that vowels and consonants are processed separately in the  
210 human brain<sup>38</sup> and that the latter are particularly important for determining word meaning<sup>39</sup>. In  
211 modern human adults with age-related hearing loss, the high frequency consonants are also the  
212 first to be affected, with a concomitant loss in intelligibility and comprehension<sup>40</sup>, demonstrating  
213 a direct link between the OBW and language comprehension. This relationship between  
214 consonant production and an extended OBW helps make the link between audition and  
215 vocalization explicit and helps explain how an extended OBW corresponds to a vocal  
216 communication system in Neanderthals that was as complex and efficient as human speech.

217 Compared to their evolutionary ancestors from the Sima de los Huesos, the  
218 Neanderthals show an increase in both the OBW and behavioral complexity, including  
219 sophisticated subsistence strategies, such as the exploitation of a wide variety of resources<sup>41-43</sup>,  
220 the systematic production and use of fire<sup>44,45</sup>, the possible construction of musical instruments<sup>46</sup>  
221 and the expression of symbolic behaviors<sup>47-50</sup>, including potential evidence for parietal art<sup>51-53</sup>.  
222 Importantly, this relationship between an increase in both behavioral complexity and the OBW  
223 was also found in previous studies of the auditory capacities in early hominins (*Australopithecus*  
224 and *Paranthropus*) and the SH hominins. The early hominins show an OBW that was similar to  
225 that in chimpanzees<sup>21</sup>, while the SH hominins show an OBW that was considerably extended  
226 compared with the early hominins, along with an increase in behavioral complexity. This  
227 increased behavioral complexity in the SH hominins includes sophisticated stone tool  
228 manufacture (Mode 2)<sup>54</sup>, evidence of communal hunting of large game species<sup>55</sup>, incipient  
229 mortuary practices<sup>56</sup> and conspecific care<sup>57,58</sup>. In our opinion, this is strong evidence in favor of  
230 the coevolution of increased behavioral complexity and increased efficiency in vocal  
231 communication throughout the course of human evolution.

232 The narrower OBW in the SH hominins, with respect to Neanderthals and modern  
233 humans, indicates that the increase in the OBW occurred in both Neanderthals and modern  
234 humans after their last common ancestor. This may have evolved through an evolutionary  
235 process of adaptive convergence for an increasingly efficient vocal communication system in  
236 both lineages. Alternatively, it could be attributed to potential gene flow between the two  
237 lineages. We would point out that the Krapina Neanderthals, who show an extended OBW  
238 similar to modern humans, are approximately 130 kya<sup>59</sup> and predate the estimated earliest  
239 evidence of gene flow between these two species<sup>60</sup>. This would seem to reject the idea that the  
240 Neanderthals acquired their extended OBW through gene flow from modern humans.  
241 Nevertheless, it would still be possible that modern humans acquired their extended OBW  
242 through gene flow from the Neanderthals. Future study of the auditory capacities in early *H.*

243 *sapiens* (i.e. older than 100 kya) can reject or reinforce this possibility. If the hypothesis of gene  
244 flow were rejected, then the only explanation for the extended OBW in both species would be an  
245 adaptive convergence for an increasingly efficient vocal communication system.

246 In summary, our results reinforce the idea that the Neanderthals possessed the same  
247 auditory capabilities as *H. sapiens* necessary to support a vocal communication system as  
248 complex and efficient as human speech. It is true that the presence of the anatomical  
249 “hardware” necessary to produce human-like speech in the Neanderthals does not necessarily  
250 imply the presence of similar mental “software” as in *H. sapiens*, and, by implication, the  
251 presence of a language with the same characteristics as that of our own species<sup>1</sup>. Nevertheless,  
252 our results, together with recent discoveries indicating symbolic behaviors in Neanderthals  
253 reinforce the idea that they possessed a type of human language, one that was very different in  
254 its complexity and efficiency from any other oral communication system used by nonhuman  
255 organisms on the planet.

## 256 **Methods**

### 257 Fossil specimens

258 *Sima de los Huesos sample (Spain)*: The site is dated to a minimum of 430 kilo-annum (ka), and  
259 the SH fossils represent early ancestors of the later Neanderthals<sup>5,32</sup>. **Cranium 3**: very complete  
260 calvarium belonging to an adolescent<sup>5</sup>, preserving both temporal bones. In this study we have  
261 used the left one (AT-4103) because it is the best preserved. **Cranium 4**: complete  
262 neurocranium belonging to an adult<sup>61</sup> preserving both temporal bones. This specimen suffered  
263 from a bilateral exostosis in both external auditory canals and was considered to have suffered  
264 conductive hearing loss<sup>62</sup>. Nevertheless, a more recent and thorough study demonstrated that  
265 the exostoses did not modify the auditory pattern of this individual<sup>32</sup> and so it can be used in this  
266 study. We have used the right side because it is slightly better preserved. **Cranium 5**: a  
267 complete adult skull preserving both temporal bones, the right malleus (AT-666) and the left  
268 stapes (AT-667)<sup>61</sup>. For this study we have used the left temporal bone because it is better

269 preserved. **Cranium 7:** Very complete calvarium of a young adult individual preserving both  
270 temporal bones<sup>5</sup>. We have used the left temporal bone (AT-804) because it is complete.  
271 **Cranium 8:** Most of the left side of a calvaria of an adult individual, including the temporal bone  
272 (AT-433)<sup>5</sup>. **Cranium 13:** Very complete calvarium of an adult individual preserving the right  
273 temporal bone (AT-2872+AT-2873). **Cranium 15:** Very complete skull of an adult individual  
274 which includes the complete right temporal bone (AT-5528). **Cranium 16:** Partial cranium of a  
275 late adolescent which preserve both temporal bones. In this study the left temporal bone (AT-  
276 6969) was used because it is the most complete one. **AT-1907:** Isolated right temporal bone of  
277 a late adolescent individual with the associated malleus (AT-3746) and incus (AT-3747)<sup>21</sup>. **AT-  
278 5518:** Isolated stapes associated with temporal bone AT-5500.

279 The bony structures of the outer and middle ear (including the tympanic cavity and the ear  
280 ossicles) are completely ossified and fully formed at birth<sup>63</sup>, and the external auditory canal  
281 reaches adult size by the age of 9 years in modern humans<sup>64</sup>. Thus, all the bony structures  
282 included in the present study have already reached their adult dimensions prior to adolescence  
283 in our own species, justifying the inclusion of adolescent individuals in this study.

284 *Neanderthal sample: Krapina sample (Croatia):* This site is dated to around 130 ka<sup>59</sup>. Two  
285 specimens have been included in this study: the adult right temporal bone Kr.38.1 (Tp.2) and  
286 the late adolescent left temporal bone Kr39.3 (Tp.4)<sup>65</sup>. **Amud1 (Israel):** This is a very complete  
287 skull of an adult individual<sup>66</sup>, including the complete left temporal bone. The age-estimates for  
288 the Mousterian levels of Amud Cave range from 50-70 ka<sup>67</sup> and the level where the Amud1  
289 cranium was found has been dated to  $53 \pm 8$  ka<sup>68</sup>. **La Chapelle-aux-Saint1 (France):** This is a  
290 very complete skull of an adult individual<sup>69</sup> and the right temporal bone was used in this study.  
291 The site has been estimated to date between 47-56 ka<sup>70</sup>. **La Quina H5 (France):** This is a very  
292 complete calvarium of an adult individual which preserves the left temporal bone<sup>71</sup>. The site of  
293 La Quina has been dated in around 48-42.5 ka<sup>72</sup>.

294 CT Parameters

295 The Neanderthals and the SH fossils were CT scanned at different institutions and at different  
296 resolutions (Supplementary Table 3). The CT scans for the Krapina Neanderthals (Kr.39.3 and  
297 Kr.38.1) were downloaded from the NESPOS platform ([www.nespos.org](http://www.nespos.org)) and the resolution is  
298 lower than that for the other fossil specimens. To ensure the accuracy of our measurements in  
299 these individuals, we have compared our values for the  $A_{OW}$ ,  $A_{TM}$  and the distance between the  
300 center of the tympanic groove and the center of the oval window in Kr.39.3 with the values  
301 previously published<sup>19</sup>, which were taken on microCT images. Our values for these variables  
302 are very similar to those published<sup>19</sup>, indicating that our measurements in this individual were  
303 not affected by the lower resolution of the CT scans.

304

#### 305 Segmentation process and anatomical measurements

306 Virtual reconstructions and metric data collection were performed using the Mimics © v.18  
307 software following the standard procedure established in previous works<sup>15,21,22</sup>. We performed  
308 semi-automatic segmentation relying on the half maximum height (HMH) thresholding protocol<sup>73</sup>  
309 to establish the boundary between the temporal bone and the air-filled cavities. This boundary  
310 was calculated as the average between the threshold for the external auditory canal and that of  
311 the mastoid air cells. Manual segmentation was necessary in the middle ear cavity of the  
312 specimen Krapina 39.3 since it was broken. In the case of Krapina 38.1 it was not possible to  
313 segment the mastoid air cells because they were filled with sediment. The anatomical  
314 measurements used to calculate the sound power transmission have been defined in<sup>15,21,22</sup> and  
315 are defined in Extended Data 8 and Extended Data 9. Most of the measures necessary for  
316 estimating the sound power transmission were taken on the 3D models using Mimics ©.  
317 However, the areas of the entry and exit of the *aditus ad antrum*, the cross-sectional area of the  
318 external auditory canal and the area of the oval window were measured in 2D images with  
319 Photoshop © v.5 (Extended Data 8).

320

## Calculation of the Sound Power Transmission and Occupied bandwidth

The use of electrical circuits to model mechanical and acoustic systems is well known in acoustic engineering<sup>74</sup>. This approach has been used by several researchers to develop electrical circuit models of the outer and middle ears<sup>75,76</sup>, which constitutes the basis of the model used in the present study. This model is a slightly modified version<sup>21</sup> of the model published in<sup>76</sup>, to take into account more recent knowledge found in the literature. The electrical circuit which models the acoustic and mechanical behavior of the external and middle ears is built with two-port sections described with 'transmission matrices'<sup>77</sup>, to make the implementation with MATLAB © R2019a easier. This comprehensive model is used to estimate the sound power transmission through the outer and middle ears as described below.

- The concha is modeled as an exponential horn. The smaller cross-sectional area is equivalent to the cross-sectional area of the ear canal.

- The ear canal is modeled as a tube with constant cross-sectional area.

- The middle ear cavity is modeled in the same way as that proposed in previous works<sup>21,75,76</sup>.

The compliance of the tympanic air space located directly behind the tympanic membrane is modeled with a capacitor, which is connected in parallel to the equivalent electrical circuit of a Helmholtz resonator representing the *aditus ad antrum* and the mastoid air cell cavities, composed of a capacitor, representing the compliance of the mastoid air cells, a resistance and an inertance, representing the *aditus ad antrum*. These parameters are calculated from physical measurements. For modeling purposes, we have considered the entrance to the epitympanum as representing the entrance to the *aditus ad antrum* and the exit into the *mastoid antrum* as representing the exit from the *aditus ad antrum* (Extended Data 8). Subsequently, we have calculated the radius of the neck of the resonator as the average between the radii at both extremes (entrance and exit) of the *aditus ad antrum*. The overall middle ear cavity model is connected in a series branch, and is an antiresonant circuit, which gives rise to a notch at the antiresonant frequency, which depends on the physical parameters.

347 - No modifications have been introduced in the tympanic membrane-malleus network, which is  
348 the same as that used in previous works<sup>21,75,76</sup>.

349 - The ossicular chain is modeled with a series branch composed of a resistance, compliance and  
350 mass, that jointly model the mass of the malleus and incus, the compliance and damping with  
351 the supporting ligaments. After that, a transformer is included, and the transformer parameter is  
352 the ratio of the malleus-incus functional lengths. A shunt branch is connected to the transformer,  
353 with a capacitor and a resistor, that accounts for the loss of stapes velocity from compression of  
354 the ossicular joints. The ossicular chain model is completed with the mass of the stapes, and  
355 another transformer, whose parameter is the stapes footplate area.

356 - Finally, the model is completed by the annular ligament block, where no modifications have  
357 been introduced compared to Rosowski's model, and the cochlear input impedance ( $Z_c$ ). The  
358 cochlear input impedance has been considered resistive, taking into account the cochlear input  
359 impedance measurements in 11 human cadaver ears published by Aibara and colleagues<sup>78</sup>,  
360 who found a flat, resistive cochlear input impedance with an average value of 21.1 G $\Omega$  from 0.1-  
361 5.0 kHz.

362 The reliability of this model was assessed in<sup>21</sup>, by comparing the theoretical middle ear pressure  
363 gain (GME) obtained for modern humans with those measured experimentally in<sup>78</sup>, finding no  
364 significant differences.

365 The electrical parameters used in the model are associated with anatomical structures of the  
366 ear<sup>22</sup>. Some of these parameters are related with skeletal structures accessible in fossils, while  
367 others are related with soft tissues which are not preserved in fossil specimens. The respective  
368 value for modern humans<sup>76,78</sup> has been used for the soft-tissue related variables which cannot  
369 be measured in fossil specimens. The use of modern human values for the soft-tissue related  
370 variables may introduce a bias in the results for the SPT (as well as the OBW) in the fossil  
371 specimens. However, previous studies<sup>14,21,22</sup> have shown that the use of these same modern  
372 human values for the soft-tissue variables to model the auditory capacities in chimpanzees does



373 not make the resultant SPT more human-like. Rather, the SPT results are fully compatible with  
374 the empirical audiogram-based results in chimpanzees<sup>14,21,22</sup>. Thus, it is reasonable to conclude  
375 that the use of modern human soft-tissue values does not bias the SPT results in the fossil  
376 specimens towards modern humans.

377 This model, where each block is modelled with transmission parameters, makes it possible to  
378 calculate the sound power at the entrance to the cochlea, assuming an incident plane wave of  
379 constant intensity stimulating the auditory system. The sound power at the entrance to the  
380 cochlea is calculated using the stapes velocity and the cochlear impedance. The results for  
381 sound power transmission presented in this paper are calculated for an incident plane wave  
382 intensity of  $I=10^{-12}$  W/m<sup>2</sup>, and are presented in dB relative to  $P_0=10^{-18}$ W.

383 The bandwidth of the external and middle ears, considered as a communication channel, is  
384 directly related to the channel capacity, an indicator of the amount of information that can be  
385 transmitted through the channel with arbitrarily low error rate. For real channels, there are  
386 different definitions of channel bandwidth that could be considered, which could provide slightly  
387 different values, but are equally useful when used for comparative purposes. In this paper, we  
388 have relied on the *occupied bandwidth*<sup>79</sup>, defined as the bandwidth such that under the lower  
389 cutoff frequency and above the upper cutoff frequency, the average power is equal to a  
390 specified percentage,  $\beta/2$ , of the total average power. In this paper,  $\beta/2$  is considered as equal  
391 to 5%, such that the occupied bandwidth includes the range of frequencies which contains at  
392 least 90% of the sound power transmitted to the inner ear.

393

#### 394 Statistical analysis

395 To test for statistical differences between samples we relied on the Exact test and we have  
396 performed a Holm-Bonferroni correction for P values for the OBW comparisons. All statistical  
397 analyses were carried out using the Past 4.02 software package.

## References

- 399 1. Tattersall, I. The material record and the antiquity of language. *Neurosci. Biobehav. Rev.*,  
400 **81**, 247-254 (2017).
- 401 2. Albessard-Ball, L., & Balzeau, A. Of Tongues and Men: A Review of Morphological  
402 Evidence for the Evolution of Language. *J. Lang. Evol.*, **3**, 79-89 (2018).
- 403 3. Dediu, D. & Levinson, S.C. Neanderthal language revisited: not only us. *Curr. Opin. Behav.*  
404 *Sci.* **21**, 49-55 (2018).
- 405 4. Bolhuis, J.J., Tattersall, I., Chomsky, N. & Berwick, R.C. How Could Language Have  
406 Evolved? *PLoS Biol* **12**, e1001934 (2014).
- 407 5. Arsuaga, J.L., *et al.* Neanderthal roots: Cranial and chronological evidence from Sima de los  
408 Huesos. *Science*, **344**, 1358-1363 (2014).
- 409 6. Arsuaga, J.L., *et al.* Postcranial morphology of the middle Pleistocene humans from Sima de  
410 los Huesos, Spain. *Proc. Natl. Acad. Sci. U.S.A.*, **112**, 11524-11529 (2015).
- 411 7. Balzeau, A., Holloway, R. L., & Grimaud-Hervé, D. Variations and asymmetries in regional  
412 brain surface in the genus *Homo*. *J. Hum. Evol.*, **62**, 696-706 (2012).
- 413 8. Pearce, E., Stringer, C., & Dunbar, R. I. New insights into differences in brain organization  
414 between Neandertals and anatomically modern humans. *Proc. Royal Soc. B*, **280**,  
415 20130168 (2013).
- 416 9. Neubauer, S., Hublin, J.J., & Gunz, P. The evolution of modern human brain shape. *Sci.*  
417 *Adv.* **4**, eaao5961 (2018).
- 418 10. Bruner, E., Manzi, G., & Arsuaga, J. L. Encephalization and allometric trajectories in the  
419 genus *Homo*: evidence from the Neanderthal and modern lineages. *Proc. Natl. Acad. Sci.*  
420 *U.S.A.*, **100**, 15335-15340 (2003).
- 421 11. Zollikofer, C. P. E., & Ponce de León, M. S. Pandora's growing box: inferring the evolution  
422 and development of hominin brains from endocasts. *Evol. Anthropol.*, **22**, 20-33 (2013).
- 423 12. Balzeau, A., Gilissen, E., Holloway, R. L., Prima, S., & Grimaud-Hervé, D. Variations in size,  
424 shape and asymmetries of the third frontal convolution in hominids: Paleoneurological  
425 implications for hominin evolution and the origin of language. *J. Hum. Evol.*, **76**, 116-128  
426 (2014).
- 427 13. Marie, D., *et al.* Left brain asymmetry of the planum temporale in a nonhominid primate:  
428 Redefining the origin of brain specialization for language. *Cerebral Cortex*, **28**, 1808-1815  
429 (2018).
- 430 14. Martínez, I., *et al.* Communicative capacities in Middle Pleistocene humans from the Sierra  
431 de Atapuerca in Spain. *Quat. Int.* **295**, 94-101 (2013).
- 432 15. Boë, L.J., Heim, J.L., Honda, K. & Maeda, S. The potential Neanderthal vowel space was as  
433 large as that of modern humans. *J. Phon.* **30**, 465-84 (2002).
- 434 16. de Boer, B. Loss of air sacs improved hominin speech abilities. *J. Hum. Evol.* **62**, 1-6 (2012).
- 435 17. Krause, J., *et al.* The derived FOXP2 variant of modern humans was shared with  
436 Neandertals. *Curr. Biol.* **17**, 1908-1912 (2007).
- 437 18. Quam, R. M., Martínez, I. & Arsuaga, J. L. Reassessment of the La Ferrassie 3 Neanderthal  
438 ossicular chain. *J. Hum. Evol.* **64**, 250-262 (2013).
- 439 19. Stoessel, A., *et al.* Morphology and function of Neanderthal and modern human ear ossicles.  
440 *Proc. Natl. Acad. Sci. U.S.A.* **113**, 11489-11494 (2016).
- 441 20. Masali, M., Maffei, M. & Borgognini Tarli, S.M. in *The Circeo 1 Neanderthal Skull: Studies and*  
442 *Documentation* 321-338 (Istituto Poligrafico e Zecca Dello Stato, Rome, 1991).
- 443 21. Quam, R., *et al.* Early hominin auditory capacities. *Sci. Adv.* **1**, e1500355 (2015).
- 444 22. Martínez, I., *et al.* Auditory capacities in Middle Pleistocene humans from the Sierra de  
445 Atapuerca in Spain. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 9976-9981 (2004).
- 446 23. Rosowski, J. The effects of external and middle ear filtering on auditory threshold and noise-  
447 induced hearing loss. *J. Acoust. Soc. Am.* **90**, 124-135 (1991).

- 448 24. International Telecommunication Union. *Recommendation ITU-R SM.443-4, Bandwidth*  
449 *Measurement at Monitoring Stations* (SM Series Spectrum Management, 2007).
- 450 25. Shannon, C.E. A mathematical theory of communication. *The Bell System Technical Journal*  
451 **27**, 379-423; 623-656 (1948).
- 452 26. Fano, R. M. The information theory point of view in speech communication. *J. Acoust. Soc.*  
453 *Am.*, **22**, 691-696 (1950).
- 454 27. Letowski, T.R. & Scharine, A.A. *Correlation Analysis of Speech Intelligibility and Metrics for*  
455 *Speech Transmission* (US Army Research Laboratory Report Aberdeen Proving Ground  
456 United States, 2017).
- 457 28. Skinner, M. W., & Miller, J. D. Amplification bandwidth and intelligibility of speech in quiet  
458 and noise for listeners with sensorineural hearing loss. *Audiology*, **22**, 253-279 (1983).
- 459 29. Kates, J.M., & Arehart, K.H. Coherence and the speech intelligibility index. *J. Acoust. Soc.*  
460 *Am.*, **117**, 2224-2237 (2005).
- 461 30. ANSI, S.3.5. Methods for Calculation of the Speech Intelligibility Index. *American National*  
462 *Standard Institute* (1997, Reaffirmed by ANSI July 12, 2017).
- 463 31. Meyer, M., *et al.* Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos  
464 hominins. *Nature* **531**, 504-507 (2016).
- 465 32. Conde-Valverde, M. *et al.* A revision of the conductive hearing loss in Cranium 4 from the  
466 Middle Pleistocene site of Sima de los Huesos (Burgos, Spain). *J. Hum. Evol.* **135**, 102663  
467 (2019).
- 468 33. Fant, C.G.M. *Speech Sounds and Features* (M.I.T. Press, Cambridge, 1973).
- 469 34. Mitani, J.C., Hunley, K.L. & Murdoch, M.E., Geographic variation in the calls of wild  
470 chimpanzees: a reassessment. *Am. J. Primatol.* **47**, 133-151 (1999).
- 471 35. Lieberman, P. *On the Origins of Language: An Introduction to the Evolution of Human*  
472 *Speech* (Macmillan, New York, 1975).
- 473 36. Maddieson, I., *Patterns of Sounds* (Cambridge University Press, Cambridge, 1984).
- 474 37. Lameira, A.R., Maddieson, I. & Zuberbühler, K. Primate feedstock for the evolution of  
475 consonants. *Trends Cogn. Sci.* **18**, 60-62 (2014).
- 476 38. Caramazza, A., Chialant, D., Capasso, R. & Miceli, G. Separable processing of consonants  
477 and vowels. *Nature* **403**, 428-430 (2000).
- 478 39. Owren, M. & Cardillo, G. The relative roles of vowels and consonants in discriminating talker  
479 identity versus word meaning. *J. Acoust. Soc. Am.* **119**, 1727-1739 (2006).
- 480 40. Divenyi, P.L., Stark, P.B. & Haupt, K.M. Decline of speech understanding and auditory  
481 thresholds in the elderly. *J. Acoust. Soc. Am.* **118**, 1089-1100 (2005).
- 482 41. Weyrich, L.S., *et al.* Neanderthal behaviour, diet, and disease inferred from ancient DNA in  
483 dental calculus. *Nature* **544**, 357-361 (2017).
- 484 42. Krueger K.L., *et al.* Anterior dental microwear textures show habitat-driven variability in  
485 Neandertal behavior. *J. Hum. Evol.* **105**, 13-23 (2017).
- 486 43. Zilhão, J., *et al.* Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science*  
487 **367** (6485) (2020).
- 488 44. Heyes P.J., *et al.* Selection and use of manganese dioxide by Neanderthals. *Sci. rep.* **6**, 1-9  
489 (2016).
- 490 45. Vallverdú, J., *et al.* Combustion structures of archaeological level O and mousterian activity  
491 areas with use of fire at the Abric Romaní rockshelter (NE Iberian Peninsula). *Quat. Int.* **247**,  
492 313-324 (2012).
- 493 46. Tuniz, C. *et al.* Did Neanderthals play music? X-ray computed micro-tomography of the  
494 Divje babe 'flute'. *Archaeometry*, **54**, 581-590 (2012).
- 495 47. Rendu, W., *et al.* Evidence supporting an intentional Neandertal burial at La Chapelle-aux-  
496 Saints. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 81-86 (2014).
- 497 48. Radovčić, D., Sršen, A.O., Radovčić, J. & Frayer, D.W. Evidence for Neandertal jewelry:  
498 Modified white-tailed eagle claws at Krapina. *PloS one*, **10** (3) (2015).

- 499 49. Jaubert, J., *et al.* Early Neanderthal constructions deep in Bruniquel Cave in southwestern  
500 France. *Nature* **534**, 111 (2016).
- 501 50. Hoffmann, D.L., Angelucci, D.E., Villaverde, V., Zapata, J. & Zilhão, J. Symbolic use of  
502 marine shells and mineral pigments by Iberian Neandertals 115,000 years ago. *Sci. Adv.* **4**,  
503 eaar5255 (2018).
- 504 51. Hoffmann, D.L., *et al.* U-Th dating of carbonate crusts reveals Neandertal origin of Iberian  
505 cave art. *Science* **359**, 912-915 (2018).
- 506 52. Pearce, D. G., & Bonneau, A. Trouble on the dating scene. *Nat. Ecol. Evol.* **2**, 925-926  
507 (2018).
- 508 53. Hoffmann, D. L., *et al.* Dates for Neanderthal art and symbolic behaviour are reliable. *Nat.*  
509 *Ecol. Evol.*, **2**, 1044-1045 (2018).
- 510 54. Carbonell, E., *et al.* Les premiers comportements funéraires auraient-ils pris place à  
511 Atapuerca, il y a 350 000 ans? *L'Anthropologie* **107**, 1-14 (2003).
- 512 55. Rodriguez-Hidalgo, A., *et al.* Human predatory behavior and the social implications of  
513 communal hunting based on evidence from the TD10. 2 bison bone bed at Gran Dolina  
514 (Atapuerca, Spain). *J. Hum. Evol.*, **105**, 89-122 (2017).
- 515 56. Sala, N., *et al.* Lethal interpersonal violence in the Middle Pleistocene. *PloS one*, **10**,  
516 e0126589 (2015).
- 517 57. Gracia, A., *et al.* Craniosynostosis in the Middle Pleistocene human cranium 14 from the Sima de los  
518 Huesos, Atapuerca, Spain. *Proc. Natl. Acad. Sci. U.S.A.*, **106**, 6573-6578 (2009).
- 519 58. Bonmatí, A. *et al.* Middle Pleistocene lower back and pelvis from an aged human individual  
520 from the Sima de los Huesos site, Spain. *Proc. Natl. Acad. Sci. U.S.A.*, **107**, 18386-18391  
521 (2010).
- 522 59. Rink, W. J., Schwarcz, H. P., Smith, F. H., Radovčić, J. ESR ages for Krapina hominids.  
523 *Nature* **378**, 24 (1995).
- 524 60. Sankararaman, S., Patterson, N., Li, H., Pääbo, S., & Reich, D. The date of interbreeding  
525 between Neandertals and modern humans. *PLoS Genet.* **8**, e1002947 (2012).
- 526 61. Arsuaga, J.L., Martínez, I., Gracia, A., Carretero, J.M. & Carbonell, E. Three new human  
527 skulls from the Sima de los Huesos Middle Pleistocene site in Sierra de Atapuerca, Spain.  
528 *Nature* **362**, 534-537 (1993).
- 529 62. Pérez, P.J., Gracia, A., Martínez, I. & Arsuaga, J.L. Paleopathological evidence of the  
530 cranial remains from the Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca,  
531 Spain). Description and preliminary inferences. *J. Hum. Evol.* **33**, 409-421 (1997).
- 532 63. Quam, R. "Temporal Bone Anatomy and the Evolution of Acoustic Capacities in Fossil  
533 Humans" PhD thesis, State University of New York, Binghamton, NY (2006).
- 534 64. Wright, C. G. Development of the human external ear. *J. Am. Acad. Audiol.* **8**, 379-382  
535 (1997).
- 536 65. Radovčić, J., Smith, F., Trinkaus, E. & Wolpoff, M. H. *The Krapina Hominids. An illustrated*  
537 *catalog of skeletal collection* (Croatian Natural History Museum, Zagreb. 1988).
- 538 66. Endo, B. & Kimura, T. in *The Amud man and his cave site.* (University of Tokyo, Japan,  
539 1970).
- 540 67. Valladas, H. *et al.* TL dates for the Neanderthal site of the Amud Cave, Israel. *J. Archaeol.*  
541 *Sci.* **26**, 259-268 (1999).
- 542 68. Rink, W. *et al.* Electron spin resonance (ESR) and thermal ionization mass spectrometric  
543 (TIMS) <sup>230</sup>Th/<sup>234</sup>U dating of teeth in Middle Paleolithic layers at Amud Cave, Israel.  
544 *Geoarchaeology* **16**, 701-717 (2001).
- 545 69. Boule, M., L'Homme Fossile de La Chapelle-aux-Saints. *Annales de Paleontologie* **6**: 111-172  
546 (1911).
- 547 70. Grün, R. & Stringer, C. B. Electron spin resonance dating and the evolution of modern  
548 humans. *Archaeometry* **33**, 153-199 (1991).

- 549 71. Martin, H. L'Homme fossile de La Quina. Archives de Morphologie Générale et  
550 Expérimentale 15. (Gaston Doin, Paris, 1923).
- 551 72. Higham, T. *et al.* The timing and spatiotemporal patterning of Neanderthal disappearance.  
552 *Nature* **512**, 306-309 (2014).
- 553 73. Coleman, M. N. & Colbert, M. W. Technical Note: CT thresholding protocols for taking  
554 measurements on three-dimensional models. *Am. J. Phys. Anthropol.* **133**, 723-725 (2007).
- 555 74. Harris, R. W. Electromechanical analogies in acoustics. *Appl. Acoust.* **3**, 265-281 (1970).
- 556 75. Kringlebotn, M. Network model for the human middle ear. *Scand. Audiol.* **17**, 75-85 (1988).
- 557 76. Rosowski, J. J. in *Auditory Computation* (Springer, New York, 1996).
- 558 77. Lampton, M. Transmission matrices in electroacoustics. *Acta Acust. United Acust.* **39**, 239-  
559 251 (1978).
- 560 78. Aibara, R., Welsh, J. T., Puria, S. & Goode, R. L. Human middle-ear sound transfer function  
561 and cochlear input impedance. *Hear. Res.* **152**, 100-109 (2001).
- 562 79. International Telecommunication Union ITU-R V.573e4, Radiocommunication Vocabulary.  
563 International Telecommunication Union Recommendations (2007).
- 

564  
565  
566 **Acknowledgments:** The authors wish to thank the following individuals and institutions for  
567 providing access to fossils and specimens housed in their care: A. Balzeau (Musée de  
568 l'Homme, France), I. Hershkovitz and J. Abramov (Tel Aviv University, Israel). CT scanning of  
569 the SH fossils was carried out at the Laboratorio de Evolución Humana (Burgos, Spain) by  
570 Rebeca García and Laura Rodríguez. Financial support for this study was provided by the  
571 Ministerio de Ciencia, Innovación y Universidades (PGC2018-093925-B-C33) of the Spanish  
572 Government. This project forms part of the Bioacústica Evolutiva y Paleoantropología research  
573 group of Universidad de Alcalá. MC-V has received a predoctoral grant from the Fundación  
574 Atapuerca. RMQ has received financial support from Binghamton University and the Ginés de  
575 los Ríos grant program from the Universidad de Alcalá. ADV has received financial support from  
576 Binghamton University and the Fulbright Commission.

577  
578 **Author Contributions** MC-V, IM, RMQ and MR designed the research and wrote the article.  
579 MC-V, ADV and CL reconstructed the 3D models for the study and collected data on the 3D  
580 models. MR and PJ modeled the hearing results. JMBC, EC and JLA provided critical  
581 comments and direct the excavation and the research project at the Atapuerca sites.

582 **Data availability:** All the technical data regarding the CT scans as well as the measurements of  
583 3D reconstructions necessary to reproduce our work are offered within the manuscript and  
584 Supplementary Information. Computed tomography scans of fossil material from Krapina are  
585 available at the Nespos platform ([www.nespos.org](http://www.nespos.org)). Computed tomography scans of the fossil  
586 specimens La Chapelle-aux-Saints 1 and La Quina H5 are the property of Musée de l'Homme  
587 (France), that for Amud 1 is the property of Tel Aviv University (Israel) and the fossil specimens  
588 from the Sima de los Huesos are property of Junta de Castilla y León (Spain), to whom  
589 application must be made for access. Interested readers may contact the authors, who will  
590 assist in getting in touch with the relevant institutions. The CT scans and 3D models of recent  
591 *Homo sapiens* are available at Morphosource ([www.morphosource.org](http://www.morphosource.org)).

592

593

594 **Competing interests:** Authors declare no competing interests.

595

596

597

598

599  
600  
601  
602  
603  
604  
605

## Figure legends

**Figure 1.** Anatomical reconstruction of the external and middle ear cavities in Neanderthals. External auditory canal (green), middle ear cavity (blue), *aditus* (orange) and mastoid air cells (purple/grey). Mastoid air cells of Krapina 38.1 (grey) is represented using the mastoid air cells of Krapina 39.3.

606  
607  
608  
609  
610  
611  
612  
613

**Figure 2.** Sound power transmission in modern humans, the SH hominins and Neanderthals. Continuous lines represent the means and colored areas show  $\pm 1$  s.d.

**Figure 3.** Occupied bandwidth (OBW) in SH, Neanderthals and modern humans. Means (triangles), medians (vertical black bars), Q1 (25%) to Q3 (75%) (boxes), and individual values (circles). Cr = SH Crania; Kr = Krapina; LCh= La Chapelle-aux-Saints1; Am1 = Amud1; LQ5 = La QuinaH5.

614  
  
615  
616

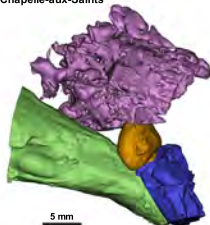
Krapina 38.1



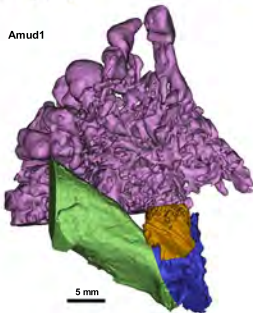
Krapina 39.3



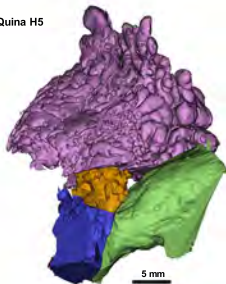
La Chapelle-aux-Saints



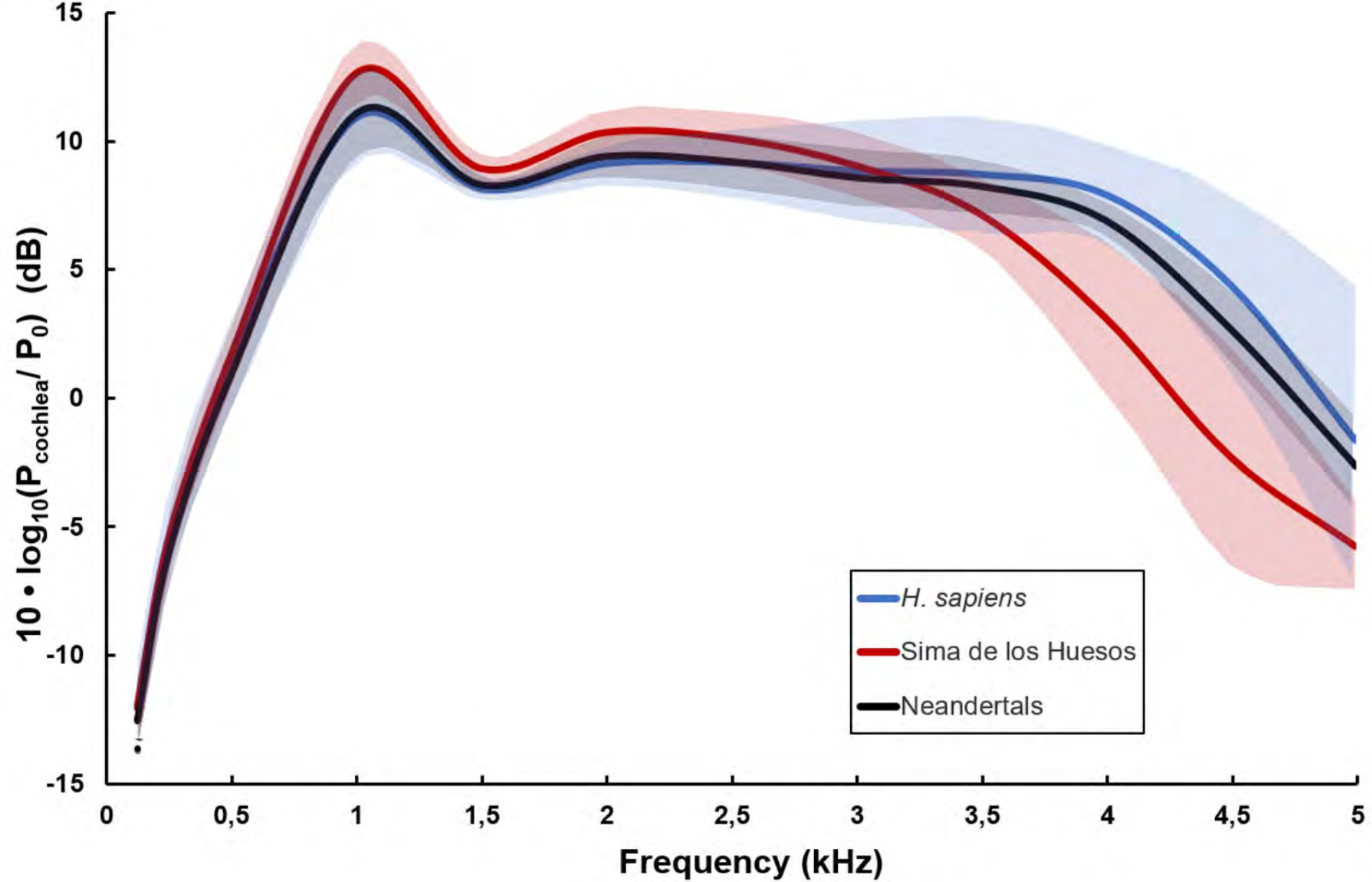
Amud1

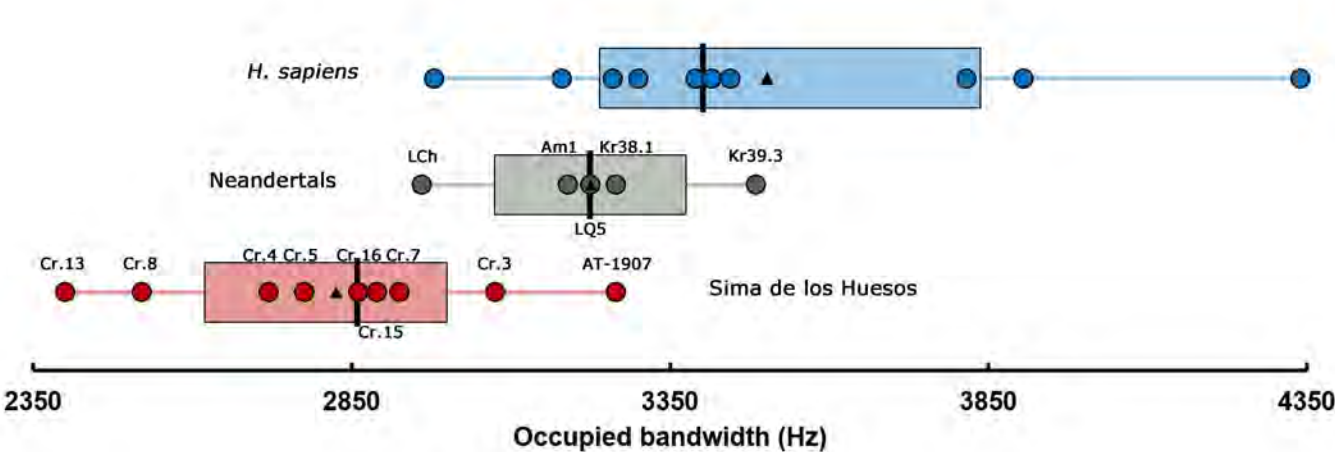


La Quina H5









617  
618  
619

**Table 1. Occupied bandwidth values and Exact test comparisons for *H. sapiens*, Neanderthals and Sima de los Huesos hominins (SH).**

	Lower limit (Hz)	Upper limit (Hz)	Bandwidth (Hz)
<i>H. sapiens</i> mean ± s.d.	813 ± 89	4316 ± 367	3503 ± 403
Range (n = 10)	660–1010	3815–5000	2980–4340
Neanderthal mean ± s.d.	810 ± 78	4035 ± 124	3225 ± 187
Range (n = 5)	715–920	3880–4200	2960–3485
SH mean ± s.d.	758 ± 60	3584 ± 242	2826 ± 264
Range (n = 9)	635–820	3170–3965	2400–3265
<i>Exact test</i>			
SH vs Neanderthals	0.280	<b>0.004</b>	<b>0.012</b>
SH vs <i>H. sapiens</i>	0.150	<b>&lt;0.001</b>	<b>0.001</b>
Neanderthals vs <i>H. sapiens</i>	0.929	0.196	0.206
<i>Holm-Bonferroni corrected P</i>			
SH vs Neanderthals	0.784	<b>0.028</b>	0.072
SH vs <i>H. sapiens</i>	0.750	<b>&lt;0.001</b>	<b>0.008</b>
Neanderthals vs <i>H. sapiens</i>	0.929	0.784	0.784

620

In bold P < 0.05