

Of Tongues and Men: A Review of Morphological Evidence for the Evolution of Language

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Abstract

Of the characteristics of the species *Homo sapiens* relative to other living animals, the use of articulated language is among the most striking. Because it implies—and allows for—complex social relationships and cognitive processes, the emergence of articulated language during hominin evolution is regarded as one of the most important steps in becoming human. Other living species have evolved complex vocalisations (e.g. songbirds) or can be trained to respond to spoken commands (e.g. dogs) and even to answer using special keyboards or sign language (e.g. great apes), but none have evolved articulated speech, and none can be taught how to talk. Tracking the emergence of language and determining which fossil hominin species used a full-fledged articulated language and which did not are somewhat of a challenge. For palaeoanthropologists and prehistorians, the timing and nature of the emergence of language—gradual or sudden, early or late in evolution—represent crucial (but missing) data when trying to interpret behaviours evidenced by the archaeological record or to define which hominins are ‘human’. A wealth of morphological and archaeological data are examined in order to put together enough clues to answer the question of when and in which species speech first evolved. Lines of enquiry include the evolution of the neural circuitry used by *H. sapiens* to produce and process speech, the anatomical specialisations which allow them to discriminate and articulate sounds, and early evidence for complex, planned behaviours and symbolic thought. This indirect evidence does not bring definitive answers about the emergence of language in the hominin evolutionary bush but illustrates that we should rethink what defines *H. sapiens* and be more cautious—or scientifically more rigorous—about what makes us supposedly unique.

Key words: paleoneurology; hominin evolution; past behaviours.

1. Introduction

Various fields of prehistoric studies are involved in trying to resolve the seemingly simple question of what makes for human specificity, if anything. From studies of morphological variation to functional morphology, and from ethno-archaeology to Evolutionary Cognitive Archaeology, data about behaviour, ecology,

morphology, and phylogeny offer wide and growingly complex insights into human and non-human natures. Language may have played a fundamental role in human evolution, as it allowed for particular social interactions, for an especially efficient teaching of skills and knowledge, and for the formulation and transmission of worldviews, identities, funding myths, etc.

Understanding the apparition and possible selection for the anatomical substrate necessary for the invention and use of speech is, therefore, a much sought-after goal in palaeoanthropology.

The volatile nature of the spoken language is of course incompatible with archaeological preservation, so that, besides studies coming out of the field of linguistics, there remains three main sources of information which can be used by prehistorians in order to approach the origins of language. The first two directly concern the biology and ecology of primates, while the third one concerns objects and evidence for complex behaviours left behind by fossil species. Behavioural and cognitive data from extant humans and non-human primates is analysed and contrasted, and correlations between behaviours and morphology are established. This evidence is dubbed ‘indirect evidence’ because it uses extant primate models in order to interpret the fossil record. Evidence for behaviours is then inferred from the morphology of fossils (‘direct evidence’), in particular from endocasts (casts of the cranial cavity which serve as a proxy for brain morphology), from the hyoid bone and modelling of the vocal tract, from chest expansion as evidenced by the spine and rib cage, and from the bony ear. The third line of evidence concerns the archaeological record and its interpretation. Complex thought processes and possible transmission of knowledge using an articulated language are, for instance inferred from the production of stone tools requiring a high degree of planning, based on experimental reproduction of flint-knapping techniques. Experimentations allow making the link between the data gathered from extant primates and data derived from the fossil record. To these sources of evidence, we may add crucial data contributed by geneticists, who have shown shared derived patterns between *Homo sapiens* and Neandertals on the *FOXP2* gene controlling for some aspects of speech production (Krause et al., 2007) as well as interbreeding between *H. sapiens* and Neandertals (Sankararaman et al., 2012).

There are two main opposing views on the emergence of language in hominins: one supports an ancient, selection-driven origin and a long, gradual development over hominid evolution (e.g. Pinker and Bloom 1990; Lieberman 2015). The other sees it as recent (in *H. sapiens* only) and sudden (e.g. Bolhuis et al., 2014). Supporters of a gradual evolution argue that the complexity and specificity of the human language make it likely to have deep roots in the hominid lineage, with elements of linguistic competence being selected individually as they gave a reproductive edge to the individuals who displayed them. On the other hand, supporters of the late sudden apparition of language as we know it, hold the

view that once a ‘language-ready brain’ (Boeckx and Benitez-Burraco 2014) had evolved, structured language was able to emerge very quickly (see Tattersall 2017 for a review of both arguments). While some prehistorians consider that evidence such as complex flint-knapping sequences is sufficient proof for the existence of a fully developed articulated language, others hold that the only suitable *terminus ante quem* for the apparition of language is the non-refutable proof for the existence of symbolic thought. This may be evidenced, for instance, by the manufacture of personal ornamentation. According to this view, symbolic objects are a reliable proxy for the existence of language because an internalised language is necessary in order to develop symbolic thoughts and behaviours (Tattersall 2017). While this makes for a very conservative estimate of the timeline of the apparition of language, it allows for a solid posterior boundary: language was likely in use by the time people started adorning themselves with symbolic, status-related objects. On the other hand, a very loose anterior boundary can be obtained by tracing back the apparition of the anatomical complexes used in the cognitive processing, vocalisation, and hearing of language in modern humans. Although the notions of primitive or full-fledged language are used regularly by prehistorians and palaeoanthropologists, it is not always clear where the border lies between the two. Bickerton (1990) defines ‘protolanguages’ as languages devoid of syntactic structure. The use of syntax can then be understood as the difference between ‘primitive’ and full-fledged language. Displaying recursion in one’s use of speech [the ability to create an infinity of different combinations with a finite number of building blocks (Hauser et al., 2002)] is a potential marker for a definition of a human-like language (e.g. Hoffecker 2007), but is also untraceable in itself in the fossil record. The use of recursion in other, longer lasting media (e.g. artistic depictions) suggests that full-fledged language has been attained. In the archaeological record, identifying indisputable instances of recursion can be tricky, and undeniable examples such as cave paintings can only provide a late boundary for the timeline of language evolution.

Anatomy, on the other hand, is used in order to track the emergence of the physical ability to produce speech.

When investigating the use of a *H. sapiens*-like language, it is Neandertals that are scrutinised the most. Because Neandertals are our closest known relatives, understanding how different or how similar they were to modern *H. sapiens* is a popular path to defining our own species. Neandertals were a large-brained species and displayed high levels of technical knowledge.

They used complex flint-knapping techniques, survived in harsh environments, and some of their behaviours point to the presence of symbolic thought (burying some of their dead, collecting unusual objects, etc.). They are, however, different from *H. sapiens* both in their morphologies and, it seems, in the relative stability of their practices through time. In particular, their prolonged use of tool-making techniques is often interpreted as a lack of innovation very much unlike the rapid technological changes seen later on in *H. sapiens*. Towards the end of Neandertal's presence in Europe, the occurrence of different types of tools and of personal ornaments in archaeological contexts otherwise attributed to Neandertals have even been interpreted as evidence for exchanges with or imitation of *H. sapiens*. This, perhaps, is more to do with our historical perception of Neandertals and of our own species than it is with archaeological evidence. Events of gene exchanges between *H. sapiens* and Neandertals (Sankararaman et al., 2012), with a small portion of Neandertal genes being passed down to modern Europeans and Asians, demonstrate close, albeit limited, reproductive contacts between the two species.

One major flaw in the conceptual framework in which Neandertals and other fossil hominins are studied, is the notion of modernity. It is used to describe certain behaviours that we can recognise in the fossil record and link to behaviours which have historically been attributed to *H. sapiens* only. If *H. sapiens*, the last surviving *Homo* species, is the only living species to do it, then this behaviour is 'modern' or 'human-like'. Because it is the most recent *Homo* species (that is to say, the last one), *H. sapiens* is often seen as the pinnacle of hominin evolution, its characters and its behaviours as the most derived and the most modern. Palaeoanthropologists have demonstrated that this is not necessarily the case, as evolution does not follow a linear course. Both *H. sapiens* and Neandertals display derived features which are not to be seen in the other species (autapomorphies).

Keeping these theoretical beacons in mind, this article will review current theories and lines of morphological evidence based on palaeoanthropological data in order to provide an overview of the possible scenarios for the apparition of articulated language in hominins. Because of the complexity of this topic and the wealth of available data, and because our space here is restricted, it is impossible to mention all the available evidence. The main focus of the article is on anatomy, as our main area of expertise is palaeoneurology. A number of issues are selected, which we hope will give the reader a sense of the current debates and how they can be addressed.

2. Brain size and encephalisation quotient

Bony anatomy offers limited but nonetheless precious clues to understanding the emergence of the anatomical substrate involved in the production of an articulated language. Among the first characters to be investigated by palaeoanthropologists was the absolute and relative size of the human brain compared with other primates and with fossil hominins. The absolute size of the human brain (on average about 1350 cm³ for extant *H. sapiens*, Beals et al., 1984) is the largest among living primates, with an endocranial volume roughly three to four times that of a chimpanzee brain (from Holloway et al., 2004's data). The brain mass of the last common ancestor between humans and great apes is estimated to have been roughly similar to that of a great ape (Sherwood et al., 2008; Alba 2010), and to that of early hominins like Toumaï and Australopithecines (Holloway et al., 2004). One of the defining criteria of the genus *Homo* being an increased cranial capacity, a difference in absolute brain size is observed around 1.8–1.5 million years ago between Australopithecines and early *Homo* representatives (Fig.1), following which a substantial increase in cranial capacity occurs in *Homo* species, up to Neandertals and *H. sapiens*. Some *H. erectus* and other fossils dated to the Middle Pleistocene (78.1 kya–126 kya) reach Neandertal and *H. sapiens* sizes, but they never reach the highest values seen in these two latter species. Mean endocranial capacities in Neandertals and *H. sapiens* are comparable [Lieberman (2011) gives an average of 1480 cm³ and 1400 cm³, respectively, in any case estimates give slightly larger averages in Neandertals compared with *H. sapiens*]. On average, cranial capacity in extant humans is roughly 20% lower than it is in fossil *H. sapiens* from the Upper Palaeolithic (40 kya–12 kya). With a general gracilisation of the skeleton comes a smaller head, and smaller brains with slightly different organisations. There is a clear trend in increasing brain size through time, while reducing the masticatory system and the relative size of the face, with the notable exceptions of the recently dated *H. floresiensis* (Kubo et al., 2013) and *H. naledi* (Dirks et al., 2017), and to some extent of the chronological variation within our species (Balzeau et al., 2013). However, there is also an increase in body size, and, therefore, a scaling effect. Jerison (1973) devised the concept of encephalisation quotient (EQ), which allows comparisons of relative brain size across species. EQ is the ratio between the average brain mass observed in a species and the brain mass that is predicted for this same species, assuming that, on average, brain mass in mammals scales to body mass to the power of two-third.

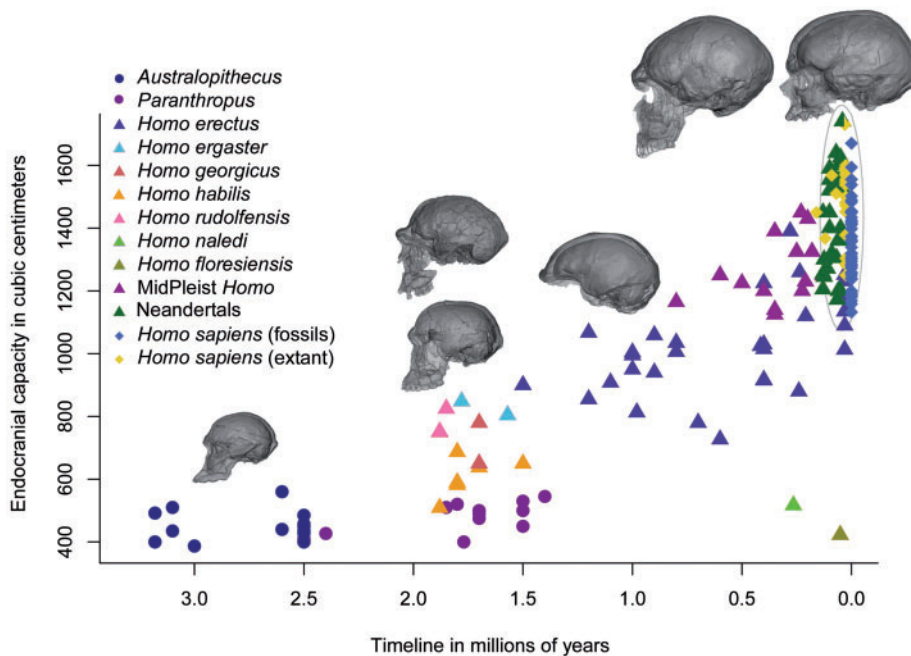


Figure 1. Variations in endocranial capacity and some hominin morphologies during the last millions of years. Data for all individuals except *H. naledi* and *H. floresiensis* are from Holloway et al. (2004). Hominin skulls and endocasts not to scale. From left to right: *Australopithecus africanus*, *H. habilis* and *H. ergaster*, *H. erectus*, Neandertal and *H. sapiens* (Cro Magnon 1).

Originally, EQ is, therefore, based on a model across mammals. For comparisons among primates, or among other groups, the scaling factor differs. One major issue when trying to compare EQ across fossil species is that the body mass of the fossils has to be estimated, usually from long bones. Long bones that are associated without doubt to a specific cranium are rarely present in the archaeological record before the generalisation of burials. Moreover, the estimations of stature and mass using the size of long bones are necessarily based on modern human and extant primate models and may be poor estimators for fossil species. EQ throughout human evolution shows trends comparable with that of absolute cerebral volume, gradually increasing through time with a steeper increase from around 1.5 million years onwards, starting with *H. erectus*, and comparable values between Neandertals and *H. sapiens* (Ruff et al. 1997). Despite a seemingly positive selection for larger brains in hominins and the implications this may have in terms of neural connections, neither endocranial volume nor EQ can be used to infer cognitive abilities or to trace back the origins of language to a particular species. Additional clues to cerebral evolution may be found in the development of functional areas of the cortex.

3. Development of language-related cortical areas

Endocranial casts are a representation of the brain covered by the meningeal layers, which makes them a reasonable proxy to estimate brain volumes and to study the external brain morphology of fossils (see Fournier et al., 2011 for an assessment of distances between brain and endocranium in extant humans). Knowing the implication of some cerebral regions in the human language through *in vivo* observations and functional neuroimaging (e.g. Vigneau et al., 2006; Byrne 2016; Pastori et al., 2016; Skeide et al., 2016), it is then possible to work backwards and attempt to identify the development of these cortical areas on the endocranial casts of fossil hominins. The morphological information derived from endocasts has one major limitation: nothing can be inferred about neural connectivity and the data is limited to the externally visible parts of the cortex. Moreover, the imprints left on the cranial bones by the cerebral convolutions are sometimes faint, and not so easy to interpret due to the presence of the meningeal layers between the brain and the inner bone table, and to inter-individual variations in the convolutional patterns.

Nevertheless, it is possible to study the emergence of a human-like pattern for the general organisation of the brain and for a number of functional areas, most importantly the Broca and Wernicke's areas. In modern humans, Broca's area (located on the third frontal convolution) and Wernicke's area [located posteriorly on the first temporal convolution (Wernicke 1874)] are both involved in speech production and processing. These areas, located on the left hemisphere, are functionally and anatomically asymmetrical (e.g. LeMay 1976). Indeed, the left hemisphere handles a disproportionately large part of language-related functions in most modern humans (although it remains rarer, the incidence of the opposite pattern is significantly more common in ambidextrous people and even more so in left-handers than in right-handers, see for instance, Knecht et al., 2000), and the Broca's caps have been shown to be asymmetrical (e.g. Balzeau et al., 2014). There is also a global pattern of asymmetry in the modern human brain, with anterior and posterior asymmetries of the hemispheres (petalias), and differences in the width of the hemispheres (Toga and Thompson 2003). The emergence of the human-like asymmetry pattern of these areas is, therefore, of interest when tracing the origins of language. However, the homology of cortical areas between species is based on their relative position to brain sulci (fissures) rather than on their cytoarchitectonics (Connolly 1936). These homologous cortical characters may thus be made up of differing Brodmann's cognitive areas, (Brodmann 1909) depending on species, so that they may not be functionally comparable (for discussions about the Broca's cap in great apes see Sherwood et al., 2003; Keller et al., 2012). Although the role of the Broca and Wernicke's areas in the production and processing of language in *H. sapiens* is demonstrated (e.g., Benjamin et al. 2017; Hagoort 2017), these areas and their asymmetry patterns are not specific to *H. sapiens* or even to *Homo* species. Anatomically homologous areas have been proposed in extant apes, so that the development of Broca and Wernicke's areas in fossil hominins cannot be assumed to imply the presence of an articulated language in the species.

A recent study found that human-like leftward asymmetries of the *planum temporale*, a cerebral region which includes the Wernicke's area, can be found not only in great apes but also in the olive baboon (Marie et al., 2017). Finding this pattern in an Old World monkey suggests that the specialisation of this area predates the split of hominids from other primates. This finding questions the direct relationship between the presence of this leftward asymmetry and the use of language functions. The presence of this shared anatomical substrate,

combined with additional anatomical and behavioural variables, likely allowed the emergence of language in humans, but its presence in fossils is not a guarantee of the use of articulated speech. This may be seen as a cautionary tale for researchers working on the development of homologous cortical areas in humans, apes, and fossil hominins, and goes to show that the *H. sapiens* cognitive abilities stem from a neuroanatomical substrate which is deeply rooted in hominin evolution. For example, Broca's area is also involved in stone tool use in monkeys and humans, suggesting that the use of language and of tools require similar computational operations and that the neural substrate involved in tool use, already present in non-human primates, could have been exapted to support language abilities in humans (Satomi et al., 2009; Uomini and Meyer 2013, see also Stout and Chaminade 2011). One further hindrance to the tracing of language origins through fossil cortical anatomy is that language processing and speech production are not constrained to Broca and Wernicke's areas, but instead activate areas throughout the cerebral cortex (Falk 2007).

4. Hearing: ear morphology

Ear ossicles are rarely recovered during archaeological excavations, because they are very small and not necessarily well preserved. They play a crucial role in hearing: the tiny malleus, incus, and staple form a chain in the middle ear and transmit sound waves to each other and into the inner ear through vibrations. This process creates pressure by reducing the area of transmission of the sound wave, and it is this increased pressure that allows the sound stimulus to be transferred efficiently through the liquid present in the cochlea (in the inner ear) rather than being muffled by the resistance of the liquid. Thanks to advances in scanning and imaging techniques, it is now possible to study the shape of ear ossicles that are still lodged in the temporal bone of fossils. Over the past few years, studies of ossicles and of the bony labyrinth have multiplied (e.g. Gómez-Olivencia et al., 2015; Beals et al., 2016; Quam et al., 2013, 2016; Stoessel et al., 2016). A dramatic increase in the amount of available comparative material is helping researchers shed light on the morpho-functional evolution of the bony ear in fossil hominins. Australopithecines may have differed from modern humans in their auditory capacities. Later on, during the Middle Pleistocene, the range of frequencies heard by *Homo* individuals seems to have been closer to that of modern humans (Martínez et al., 2013; Quam et al., 2015). This is evidenced by the morphology of the outer and middle ear of the Sima de les

Huesos fossils (Sierra de Atapuerca, Spain), which are dated to around 530 kya (Bischoff et al., 2007) and thought to be either Neandertal ancestors (Arsuaga et al., 2014) or early Neandertals (Meyer et al., 2016). Quam et al. (2015) compared the estimated auditory capacities of Australopithecines, the Sima de los Huesos fossils, chimpanzees, and modern humans, using outer and middle ear anatomy (including the ossicles). They found that Australopithecines showed a derived condition compared with chimpanzees, with a shift to hearing higher frequencies like the Sima de los Huesos hominins and modern humans do, but a narrower range of perceived frequencies, this time similar to chimpanzees. This, together with heightened sensitivity to some frequencies, could be an adaptation to ‘short-range vocal communication in open habitats’. The shift to the condition observed in modern humans seems to have been underway before the split between Neandertals and *H. sapiens*, with the Sima individuals showing an intermediate position, with better adaptations to hearing the range of frequencies required for human speech than seen in chimpanzees or Australopithecines.

One major line of enquiry followed by palaeoanthropologists concerns Neandertals’ ability to hear and to produce the same range of sounds as modern humans can, and whether or not they were as efficient as *H. sapiens* in their use of speech (for a recent assessment of genetic and cultural evidence arguing for modern-like speech in Neandertals, see Dediu and Levinson 2013). In recent years, a number of Neandertal ear ossicles have been discovered in the temporal bone of previously known specimens thanks to imaging methodologies (Fig. 2). These also allowed the investigation of the shape of the bony labyrinth, which is involved in translating the vibrations transmitted through the middle ear into signals. Neandertal ossicles show substantial differences to those of *H. sapiens*. Morphometric comparisons between Neandertal, *H. sapiens* and great apes suggest that the ear ossicles are more derived in Neandertals than they are in *H. sapiens* (Stoessel et al., 2016) but the authors conclude that this may be due to covariation with the shape of the temporal bone in which the ossicles are located, and that the influence of this variation on auditory capacities is probably limited.

5. Vocalising: morphology of the larynx, pharynx, and oral cavity

Although researchers have shown interest in the anatomy of the speech-producing apparatus since the 19th century (see Lieberman 2012), the modalities of the complex evolutionary history of the human larynx,

pharynx, tongue, and oral cavity are not yet fully understood. It is clear, however, that none of these anatomical elements evolved solely ‘for’ speech as they are primarily involved in the vital functions of eating and breathing. Several anatomical areas of interest can be identified when studying the vocalisation process, which Nishimura et al. (2006) summarise as follows: ‘the lungs [, whose size and shape is evidenced by the rib cage,] generate sound power, the vocal folds in the larynx comprise the sound sources, and the SVT [(Supra-laryngeal vocal tract)] resonates the sources to generate voiced sounds [...]’. Skeletal remains can be used in order to determine if and to what extent fossil hominins were able to engage in articulated speech. One major hindrance is the paucity of the fossil record: the non-bony anatomy such as the soft palate, the tongue, or the trachea and the cartilaginous elements are irremediably missing. The hyoid bone is extremely rarely fully preserved and virtually never in association with the cranium (the *Dikika Australopithecine* being the only exception to our knowledge). However, when the face and the mandible are preserved, the oral and nasal cavities may be studied, as well as attachment sites for the tongue and a number of muscles involved in moving the hyoid bone and the larynx (for a list of muscles, attachment sites, and actions see Lieberman 2012). In modern humans, a low position of the larynx, a short face and a round tongue are thought to enhance speech abilities (Lieberman 2012) and must have been selected for because they give a decisive advantage, as this position of the larynx is also associated with increased choking risks (Lieberman 2012). A wealth of studies have shown that this advantage concerned feeding (Hiimae et al., 2002; Boë et al., 2013) and swallowing (Lieberman et al., 2001) functions. These adaptations were, therefore, likely diverted towards the use of speech, rather than driven by it. Nishimura et al. (2006) have shown that the characteristic proportions of the adult human supra-laryngeal vocal tract (SVT) are associated with two major features: the descent of the larynx relative to the palate, and the flattening of the face. The association of these two features gives the human SVT’s horizontal oral cavity and vertical laryngeal cavity their similar lengths, and these proportions come with characteristic resonance properties. The authors found that only one of these two features is unique to humans: the descent of the larynx during early childhood is shared with chimpanzees, while the flattening of the face is not. If human proportions in the SVT were achieved through two separate evolutionary mechanisms, it is likely that these adaptations were indeed primarily driven by another function, and ‘secondarily advantageous’ for speech in

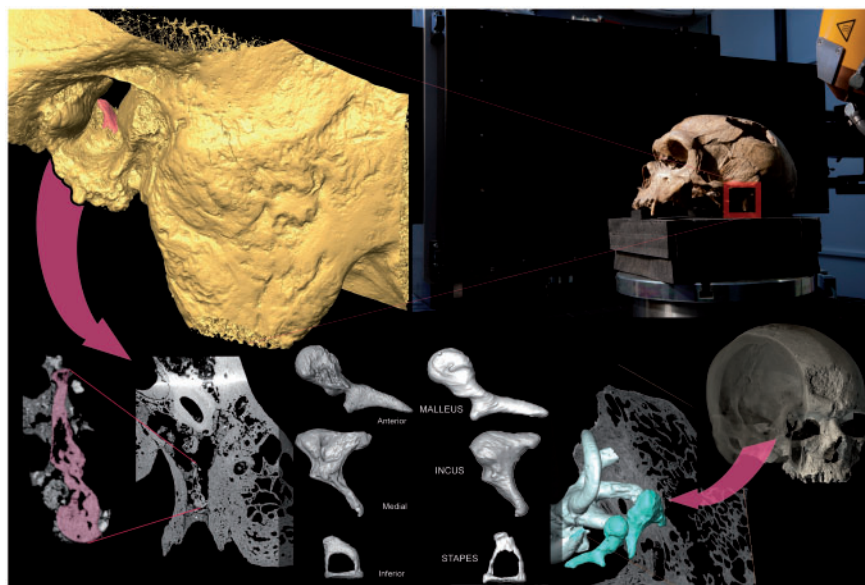


Figure 2. Microtomographic acquisitions at the AST-RX platform (UMS 2700, MNHN and CNRS) and identification of new ossicles within the temporal bones of the La Chapelle aux Saints and La Ferrassie 1 Neandertals (left) and of the Upper Palaeolithic skull Cro Magnon 1 (bottom right).

humans (Nishimura et al., 2006). The authors rightly stress that it is not the study of one key feature which is likely to bring the best answer to speech evolution, but rather multifocused approaches.

On the Neandertal front, there is an ongoing controversy about whether or not Neandertals were able to produce similar speech to *H. sapiens*. Researchers have been using modern human and non-human primate models in order to try and reconstruct fossil vocal tracts—a difficult task in the absence of soft tissues in fossils. Starting in the 1970s, Lieberman et al. (1972) have argued that the vocal tract of Neandertals would not have allowed them to produce a similar range of sounds as *H. sapiens* with equal efficiency (for a more detailed review of these works see Lieberman 2012) and that Neandertals were ‘not as well equipped for language as modern man’ (Lieberman et al. 1972). This is not to say that they were completely deprived of articulated speech (Lieberman and Crelin 1971). This hypothesis was originally based on the reconstructed position of the hyoid bone in Neandertals as being higher than it is in modern humans. This conclusion, however, was reached by drawing parallels between human newborn and Neandertal anatomies, which is highly controversial.

The hyoid bone is located at the level of the mandible and the third cervical vertebra, and is only attached to the rest of the skeleton by muscles and ligaments.

Muscles involved in tongue, larynx, pharynx, and epiglottis movement are attached on the hyoid. Because it does not have articular facets that match with those of other bones, its position relative to other bones in fossil skeletons can only be hypothesised (e.g. Boë et al., 2006; Granat et al., 2006). This in turn gives rise to differing arguments about the position of the cartilaginous and soft tissues which are attached to the hyoid bone, and about articulatory capacities in fossil species. Several attempts have been made to reconstruct a Neandertal vocal tract using different methodologies, but all of them have necessarily had to rely on *H. sapiens* models applied to composite Neandertal remains (the only complete Neandertal hyoid known so far being that of the Kebara 1 individual, which frustratingly is lacking a cranium). Some researchers are testing models using a variety of positions for the hyoid bone and for the larynx (e.g. Barney et al., 2012; Boë et al., 2013). Boë et al. (2002) and Boë et al. (2013) used an articulatory model to simulate vowels with different larynx positions and conclude that vowel contrast can also be realised if the larynx is in a higher position compared with *H. sapiens*, a position which has been hypothesised by some workers. Barney et al. (2012) attempted to predict articulatory capacities in Neandertals using a reconstructed vocal tract and testing the results with different hyoid and mandible positions. Estimations of the extent of the differences in vowel space for *H. sapiens* and

Neandertals differ depending on the authors and the models used.

Concerning hyoid anatomy, only two complete hyoid bones are known from the fossil record, but recent work suggests that the body of the hyoid was derived in the Sima de les Huesos individuals, showing a similar condition in pre-Neandertals and Neandertals as in *H. sapiens*. In comparison, Australopithecines seem to exhibit an ‘ancestral’ chimpanzee-like morphology (Martínez et al., 2008). Similarly, Steele et al. (2013) found that the Dikika (Australopithecine) hyoid is comparable with the chimpanzee morphology, whereas the Kebara (Neandertal) specimen is closer to the *H. sapiens* morphology. The authors hypothesise that the presence of an expanded bulla on the hyoid corpus of African apes (gorillas and chimpanzees) is linked to the way in which air sacs sit against the posterior part of the hyoid body. The authors point out that although the function of the laryngeal air sacs in gorillas and chimpanzees is unclear, other researchers have suggested that their presence would hinder the efficiency of speech communication by adding resonances to the vocal signal (e.g. De Boer 2009). The absence of a bulla on the hyoid corpus in the *H. sapiens*, Neandertal, and Sima specimens could then be linked to the loss of air sacs before the split between the Neandertal-*sapiens* lineages, which suggests a possible selection against speech hindrance in humans (De Boer 2009). This does not prove the capacity for speech in the Sima or Neandertal individuals. However, the data from this study and others (e.g. Martínez et al., 2013) are an accumulation of evidence in favour of a bony anatomical substrate for hearing and speaking, which is either present or undergoing evolution towards a *H. sapiens*-like pattern in (pre?)Neandertals 530 kya ago, around or after the split between Neandertals and *H. sapiens*.

Aside from anatomy, advances in the understanding of speech abilities in primates are coming increasingly from *in vivo* observations. Independent studies examining ‘indirect’ data from a captive orangutan and a captive gorilla suggest that great apes have the ability to learn calls and perform breathing behaviours (like ‘raspberries’) that are outside of their species-specific repertoire when exposed to humans, by exercising control over their vocal folds and their lips (Perlman and Clark 2015; Lameira et al., 2016). This has, so far, only been observed in isolated specimens, but it is likely that these recent studies will lead to additional data being collected from captive great apes. The split between orangutans, gorillas, and *H. sapiens* is estimated around 10 million years ago, and documenting these abilities in great apes suggests that modern humans’ fine control

over their vocal folds and vocal apparatus could be built on a substrate which precedes the genus *Homo* by millions of years.

6. Discussion

6.1 Conceptual frameworks for the timeline of language evolution

The timeline of the apparition of language can only be approached in palaeoanthropology through the prism of linguistic theories, whether or not they are explicitly acknowledged. Behind the contentious theory of the late and sudden apparition of language during human evolution, lies the idea that an ‘internal language’ (Chomsky 2010) is ‘the fundamental basis of human symbolic thought with communication a mere byproduct’ (Corballis 2017). The apparition of language is then considered to be directly linked to a shift to symbolic thinking, and concomitant to the apparition of symbolic behaviours. On the other hand, the theory of a gradual development of language driven by selection is based on the Darwinian theory of selection for advantageous traits (see for instance Pinker and Bloom 1990), which makes it a stronger candidate from the standpoint of palaeoanthropology. If language is conceptualised as a form of communication instead of thought (Corballis 2017), then it cannot be argued that it exists only in *H. sapiens*. It is also unlikely that it appeared suddenly, given that various forms of communication are known in animals. It then follows that the emergence of language must be linked to the advantages conferred by this tool for passing on knowledge. The corollary of this theory is that the use of an articulated language can have preceded the emergence of symbolic behaviours by a long time, and even more so the apparition of symbolic artefacts in the archaeological record. One of the bases of this hypothesis is the apparent grade shift in skeletal morphology from *Australopithecus* and *Paranthropus* species to *Homo* species. Another main tenet is that spoken instructions would have helped tremendously in the transmission of flint-knapping skills, starting with Oldowan tools (first recorded around 2.6 million years ago) and becoming more sophisticated with Acheulean handaxes (1.7 million years ago) long before the advent of *H. sapiens*. Recent works, however, suggest that aspiring flint-knappers learn to produce bifaces more efficiently, at least initially, when no vocal instructions are used in the teaching (Putt et al., 2014). This may not be the case for Levallois débitage (a knapping technique in which a flake of desired shape is obtained after preparation of the core), which was practised by Neandertals and which demands a high amount of foreplanning.

In general, the soundness of deriving information about the use of language from the complexity of flint-knapping sequences remains debatable (Gowlett et al., 2012). Some authors support an early presence of some form of rudimentary speech, with full-fledged language appearing suddenly in *H. sapiens* (Klein, in press). For Klein, full-fledged language appeared relatively recently in the evolution of *H. sapiens*: around 50–40 kya, in Africa. That is to say, more than 150 kya after the first known *H. sapiens* fossils appear in the record. Language is then linked to the first ‘indisputable’ appearances of art and personal adornment. It is worth noting, however, that earlier instances of such symbolic behaviours have been proposed [for instance, the assemblages of Nassarius shell beads at numerous cave sites in the Témara region of Morocco, among which Taforalt Grotte des Pigeons (between 60 and 85.5 kya) and Ifri n’Amar (around 83.3 kya, d’Errico et al., 2009); at Blombos cave in South Africa with shell beads and incised pieces of ochre dated to 75 kya (d’Errico et al., 2005; Henshilwood et al., 2009); or at Diepkloof cave in South Africa, with ostrich shells showing abstract engravings and dated to 60 kya (Texier et al., 2010)].

6.2 Lines of evidence

There are two main ways to approach the evolution of language based on endocranial anatomy: one is to attempt tracing, in the fossil record, the origins of anatomical specialisations known to play a role in speech production in extant humans. This does not imply a particular *a priori* knowledge of the species with which language first appeared. The other is to start from an assumption about the species in which *H. sapiens*-like language evolved, based on the archaeological record, in order to define which cerebral re-arrangements might be key in allowing for this language capacity to develop [see, for instance, Boeckx and Benítez-Burraco (2014) for such an approach linking the language-ready brain to the *sapiens*-specific globular endocast]. While both approaches carry inherent biases (i.e. comparing anatomically homologous features which may not be functionally homologous, or choosing a starting hypothesis which may be erroneous), both contribute valuable information to the understanding of the evolution of the human brain.

Several lines of morphological evidence can be brought into the debate on the origins of language and have been addressed here separately. However, the presence of the derived, *H. sapiens*-like state on one or even all of these characters does not necessarily attest of the use of language. Rather, it attests of the presence of the necessary conditions for its emergence. The reverse is also true.

The absence of the characteristics as observed in *H. sapiens* does not preclude the existence of a complex language.

7. Conclusion

In the search for the origins of speech in fossil hominins, anatomy and genetics offer crucial evidence. The two bigger-brained *Homo* species, *H. sapiens* and Neandertals, share a number of characters such as cerebral asymmetries, similar auditory capacities and mutations on the language-involved *FOXP2* gene. They also show striking differences in cerebral organisation, reflecting different adaptations to their respective cerebral enlargement processes. Genetic admixture suggests ties between Neandertals and *H. sapiens*, and probably a capacity to communicate. Archaeological clues suggest that Neandertals were organised in social groups, displayed elements of ritual behaviour, and used technological and subsistence strategies that all point to a complex communication system. How complex exactly, and how similar to *H. sapiens*, seems to remain a matter of personal conviction on the part of prehistorians—fluctuating on a spectrum according to whether we give more credit to Neandertal’s behavioural similarities with *sapiens* or to their differences. When it comes to the articulated language in Neandertals (and even more so for other fossil hominins), anatomical evidence alone cannot allow for the definite certitude that it was present. Perhaps more interestingly, the evidence cannot allow us to refute it either. These recent advances in palaeoanthropology force us to rethink the place of *H. sapiens* and its behaviours in a wider evolutionary context. For further insights into the origins of language itself, these advances in the understanding of fossil morphologies must continuously be reviewed against the growing archaeological evidence for past human behaviours, ancient DNA, and linguistic theories.

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