



Neanderthal language revisited: not only us

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Here we re-evaluate our 2013 paper on the antiquity of language (Dediu and Levinson, 2013) in the light of a surge of new information on human evolution in the last half million years. Although new genetic data suggest the existence of some cognitive differences between Neanderthals and modern humans — fully expected after hundreds of thousands of years of partially separate evolution, overall our claims that Neanderthals were fully articulate beings and that language evolution was gradual are further substantiated by the wealth of new genetic, paleontological and archeological evidence briefly reviewed here.

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Current Opinion in Behavioral Sciences 2018, 21:49–55

This review comes from a themed issue on **The evolution of language**

Edited by **Christopher Petkov** and **William Marslen-Wilson**

<https://doi.org/10.1016/j.cobeha.2018.01.001>

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Introduction

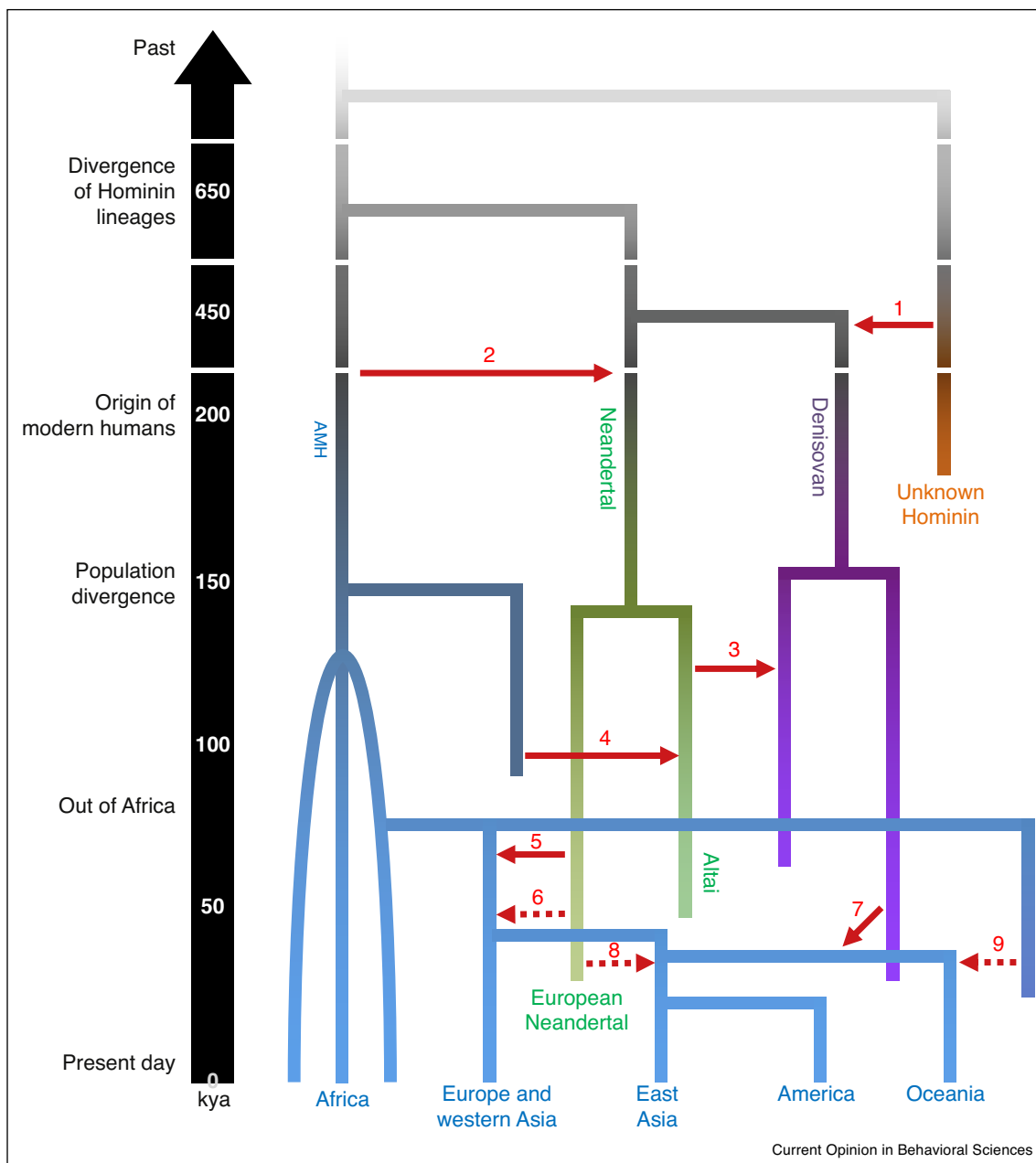
In 2013 we published a paper [1] arguing that vocal language has had a long and gradual evolution in the 1.5 my since *Homo erectus*, and that Neanderthals were articulate humans, not very different from us. We marshaled paleontological, archeological and genetic evidence against the saltationist view that language evolved abruptly within the last 100 ky (e.g. [2]). Since then there has been a flurry of new evidence from paleontology, archeology and ancient DNA that, we argue here, largely supports our views of a much deeper antiquity and gradualism.

The human tree

One striking finding is that many human lineages were coexisting just 300 kya (including *Homo naledi*, *Homo floresiensis*, Denisovans, Neanderthals and even anatomically modern humans [3^{*}]), another being the degree of reticulation in the human tree evidenced by genetics. Recent data suggests that at least 50 ky of interactions on a vast geographic scale from the Levant to Siberia and Western Europe gave plenty of scope for interbreeding; **Figure 1** shows some of the gene flow across the Neanderthals, Denisovans and ourselves.

The ancestors of Neanderthals and Denisovans left Africa c. 650 kya, and by 450 kya had diverged into these two lineages, and there are indications of early Neanderthal and Denisovan interbreeding [4], and of interbreeding between Denisovans and yet another archaic hominin. The Neanderthals then interbred with anatomically modern humans (AMH) on at least three occasions, likely when AMH first came into the Levant 100–120 kya [5^{**},6], and also during AMH's move into glacial Europe (c. 50 kya [7]). For example, a Siberian Neanderthal has AMH genes introgressed c. 110 kya [7], and an early AMH with Neanderthal anatomical features c. 40 kya from Romania [8] had Neanderthal ancestry just 4–6 generations before [9]. Recent data suggests that while Neanderthals and Denisovans clearly form a clade, the mtDNA groups the former with AMH due to their original mtDNA being replaced by an AMH-like lineage probably through interbreeding before c. 270 kya [10]. It is now clear that such interbreeding did leave traces in contemporary modern humans outside Africa at the level of a few percent of the genome, with regional and inter-individual variation probably due to repeated interbreeding with Neanderthals and Denisovans [5^{**},11^{**},12^{**}]. Contact between human lineages is also revealed by other lines of evidence including the oral commensal microbe *Methanobrevibacter oralis* from a Spanish Neanderthal pointing to his ancestors having had contact with an African strain presumably from the AMH in the Levant c. 126 kya [13], and the sexually transmitted oncogenic *human papillomavirus 16* which shows strains having split c. 450 kya mirroring the divergence between Neanderthals and AMH, but later with the Neanderthal strain re-infecting AMH after c. 120 kya [14]. Leaving aside the functional relevance of these genomic introgressions for now, what they overwhelmingly highlight is the interwoven histories of the human lineages within and outside Africa during the last half million years.

Figure 1



Schematic representation of human evolution (based on [15^{*}]) focusing on the lineages leading to ourselves (blue), Neanderthals (green) and Denisovans (magenta) and highlighting probable interbreeding (numbered red arrows). 1: 2.5–5.8% Denisova genome from archaic hominin having diverged 0.9–1.4 mya [16]; 2: mtDNA introgressed c. 270 kya into a Neanderthal (Hohlenstein-Stadel, Germany) from an African lineage leading or related to AMH [10] (see also [4]); 3: at least 0.5% genome coming from a Neanderthal population closer related to the Altai Neanderthals [16]; 4: 1.0–7.1% gene flow from AMH into Altai Neanderthals [7] (see also [9]); 5,6,8,9: multiple introgressions from Neanderthals into various modern human populations outside Africa resulting in about 2% (regionally and inter-individually variable, slightly more in East Asia) Neanderthal DNA [5^{**},11^{**},12^{**}]; 7: Denisova introgression resulting in about 2–4% Denisovan DNA in Melanesia (less in e.g. South Asia [5^{**},12^{**}]).

Functional genetic differences between AMH and Neanderthals

With almost 20 partial or full Neanderthal genomes in hand, the differences between ‘us’ and ‘them’ are quantitatively very modest indeed (e.g. [16] page 48 state that

there are ‘96 fixed amino acid substitutions in a total of 87 proteins and in the order of three thousand fixed changes that potentially influence gene expression’), but they might potentially have high functional relevance and complex, often indirect and still poorly understood

phenotypic consequences. For example, some of these genes with fixed changes are expressed in the developing neocortex [16], other are involved in skin, hair and bone structure, while others affect the immune and reproductive systems [11,17^{**}]. Nevertheless, it is now possible to explore the function and evolutionary fate of archaic introgressions in a ‘fossil-free’ manner by examining the introgressions in modern populations [17].

For understanding language evolution in particular, the genes involved in brain development and the vocal organs are of course especially interesting but, unfortunately, linking molecular genetics to language and speech is an extremely complex endeavor [18,19]. Thus, there has been only slow progress in understanding the functional implications of the non-coding differences between modern and archaic humans in the ‘star’ gene *FOXP2* (such as the *POU3F2* putative binding site in intron 8 [20]), but it seems likely that non-coding changes in this and other language-implicated genes such as *ROBO1*, *ROBO2*, and *CNTNAP2* rose to high frequency after the separation of AMH from archaic hominins [21]. However, these genes are expressed not only in the brain, increasing the difficulty of attributing these putative selective pressures to language and speech.

Another approach is to locate sequences of archaic DNA that have increased in frequency or, more often, that have been systematically purged from the modern genome, and try to understand their functional implications. These ‘genomic deserts’ from which archaic DNA seems to have been eliminated [5^{**},12^{**},22^{**}] are (mostly non-coding) regions located preferentially near protein-coding genes [22^{**}], evolutionarily conserved regions [12^{**},23^{**},24], genes involved in brain development [5^{**}], including *FOXP2* [5^{**},12^{**}], and genes expressed in the testes and in meiotic germ cells and potentially relevant for male hybrid sterility [11^{**},12^{**},25^{**}]. The most plausible explanation for this loss of archaic DNA is negative selection [5^{**},12^{**}], an inference reinforced by other lines of evidence including the tissue-specific (especially in the brain and testes) downregulation of introgressed archaic DNA [26^{**}] and the association of some archaic sequences with various pathologies [27^{**}] in existing humans, possibly resulting from a combination of genomic incompatibilities [5^{**},12^{**}] and many weakly deleterious alleles becoming visible to purifying selection after introgression in the larger AMH population [23^{**},28^{**}]. However, the pattern is not all about loss: there are regions of archaic DNA that have dramatically increased in frequency, especially near genes involved in immunity [5^{**},29–33], metabolism [5^{**},12^{**}] and skin, hair and bone phenotypes [5^{**},11^{**},32,34], pointing to advantageous adaptations developed by the other hominins in their non-African environments [32,33,35^{**}]. In understanding these patterns, it is important to remember that Neanderthals were a heavily inbred population (the Altai

individual’s parents were related as half-siblings) with very low effective population sizes (possibly by an order of magnitude lower than the early AMH’s), which may have lowered their fitness by as much as 40% [7,23^{**},28^{**}].

One interesting development has been the exploration of the genes involved in the reduction of facial prognathism, dentition and jaw, and the correlated globularization of the brain, a process that extends over 2 my of human evolution and that has traditionally been viewed as related to changes in diet, cooking and technology. However, the last stages of the process, and the transition from Neanderthal to AMH skull-shape (more globular), might have been driven by language. Some authors argue that globularization may have originated in ‘self-domestication’ with associated neotenization, affording better neural connectivity, and they highlight wide networks of genes potentially involved in this process [36–39]. However, the recent reanalysis of 300 ky early AMH skulls from Morocco shows that these skulls do not have a fully globular shape despite their fully modern faces [3^{**},40^{**}]. Other researchers argue that facial reduction may have been driven by speech, more precisely by the optimization of the 1:1 oral versus supralaryngeal vocal tracts proposed to be crucial for speech production [41,42]. Exciting recent comparisons of methylation patterns between modern and archaic humans ([43], D Gokhman *et al.*, <https://www.biorxiv.org/content/early/2017/10/03/106955>) found that modern human-specific changes preferentially affect the face, the vocal tract (especially the larynx) and the pelvic region, suggesting that there were further changes in our lineage, after the split from the Neanderthals, possibly affecting vocal tract anatomy and physiology. Nevertheless, even if these changes did affect (or even evolved in response to) speech production, they suggest that probably our lineage tweaked an already-existing speech production apparatus instead of suddenly evolving a new one from scratch.

Neanderthal cognition as evidenced by archeology

Neanderthals once covered a vast and climatically and ecologically diverse range, from Siberia to Gibraltar, and contrary to earlier stereotypes, they did adapt their diet and technology to local conditions [13,44]. In northern latitudes, they were predominantly carnivorous, had advanced leather processing technology (using *lissoirs*, probably later borrowed by AMH [45]), with modeling studies suggesting advanced winter clothing [46] using stone and bone awls (such as found in the Grotte du Renne) as sewing aids [47], but in general their diet was apparently very flexible and adapted to the local environment, including both meat and vegetable foods [48] to varying proportions [13,49–51]. Bitter medicinal herbs were consumed [52], a Neanderthal with dental abscess appears to have treated himself with poplar bark (a source of salicylic acid) and possibly mold-produced antibiotics

[13], and there are indications of possible dental manipulations [53] — all suggesting medicinal expertise.

The purported differences in technology between AMH and Neanderthals now appear much smaller following the clear association of the *Chatelpéronian* at the Grotte du Renne with the Neanderthals [54*], new analyses suggesting that there were no differences in raw material efficiency [55], that bone was used for tools [56], that hafting might go back to 240–270 kya [57] and that manganese dioxide was used to produce fire on demand 50 kya [58], and only after c. 40 kya (as the Neanderthals were disappearing) did AMH technology become clearly superior.

One critical question has been whether there are any traces of Neanderthal symbolic activity, with earlier potential examples often been dismissed as excavation or dating errors. However, the unequivocal recovery of Neanderthal DNA at Grotte du Renne [54*] seems to connect them, the advanced *Chatelpéronian* technology, and the elaborate necklaces of animal teeth and shells found there (but see [59]). Recently, a cave in Spain, apparently used as a mortuary site involving fire and hunting trophies but not inhabited, has yielded Mousterian layers containing numerous small hearths with over 30 antlers and horn-cores associated with an infant burial (E Baquedano *et al.*, Session 7, ESHE 2016, Madrid). There are suggestions that Neanderthals at several sites may have used long bird feathers for personal adornment [60], but probably the most spectacular recent findings are the c. 40 kya decorated raven wing bone from Crimea [61] and the c. 170 kya circular constructions from broken stalagmites (collectively weighting more than two tones) more than 300 m deep in the Bruniquel cave [62], for which it is hard to imagine any reason other than ceremonial.

Inferences concerning language and speech

In what follows we adopt the view that language involves a cognitive architecture that maps sounds (or gestures) into meaning through a series of combinatorial structures, while insisting that language is also a motoric and perceptual skill. Due to the fact that existing languages vary widely in their organization, it is not possible to be very precise about the general properties of those structures, except that they involve a series of transductions across levels of representation (e.g. phonetics, phonology, morphology, syntax, semantics, pragmatics) without 1:1 mappings. Not all languages, for example, exhibit phrase structure at a surface level [63], but developed languages probably all involve hierarchical and recursive structure if not at a syntactic level, then at a semantic and pragmatic one. The critical function is to render propositional content and associated illocutionary force into a perceptual medium, with content recoverable with the aid of contextual inference. Although the inference of prehistoric linguistic structure will always be indirect, the fact that advanced technology itself involves hierarchical and

recursive structure (as in the manufacture of a composite tool) provides circumstantial evidence for the existence of the planning, memory and motor skills also involved in language [64]. Language affords culture-carrying capacity (e.g. there are no advanced technologies without language), and this linkage allows reasonable inferences from the archeological record [65]. Therefore, we think it is overwhelmingly likely that Neanderthals were as much articulate beings as we ourselves are, that is, with large vocabularies and combinatorial structures that allowed propositional content and illocutionary force to be conveyed. Only such an advanced communication system could have carried the advanced cultural adaptations that Neanderthals exhibited. However, some of the new findings, especially those coming from the genetics of brain development and neurocognitive disorders, seem to strongly suggest that, despite a profound shared humanity, archaic and modern humans were not identical [66].

The arguments for speech given in our 2013 paper still hold: Neanderthals had the modern (or near-modern) vocal apparatus ([43], D Gokhman *et al.*, <https://www.biorxiv.org/content/early/2017/10/03/106955>), breathing control, and acoustic sensitivity (audiograms) involved in modern speech. Since then, there is better evidence that the Neanderthal cochlear volume and audition were similar to modern humans and different from the chimpanzees [67], that despite differences in the morphology of the ear ossicles (probably due to differences in cranium) they were functionally very similar probably due to selective pressures for the maintenance of the same auditory profile [68*], while the biomechanical modeling of the Kebara 2 Neanderthal hyoid showed that it is extremely similar to the modern human one in more than just shape [69**].

Neanderthals had elaborate cultural adaptations that were virtually identical to AMH (until the latter developed the Upper Paleolithic toolkit after the demise of the Neanderthals), they flexibly adapted to their ecologies, buried their dead (apparently with mortuary ceremonies), built large structures, penetrated deeply into caves, and seem to have adorned themselves with drilled beads and feathers. They inhabited a climatic range (from Arctic to Mediterranean) requiring the extended ability to use culture as a buffer for ecological adaptation, and they interacted repeatedly with AMH over tens of thousands of years, exchanging genes, parasites and culture.

It will always be hard to prove the existence of prehistoric language and to infer its properties beyond the 10ky range of historical linguistics [70]. Almost no-one doubts AMH had language 60 kya just before the great diaspora, since all branches of humankind have language, but how far back should we project it? The evolution of language involved very probably a complex interplay between

exaptation, reorganization, phenotypic plasticity, adaptation and cultural evolution, touching many components and processes, requiring tens or hundreds of thousands of years and proceeding at highly variable rates [1,71–73]. The ‘externalization’ of language and its neural underpinnings, far from being trivial, is, in our view, one of the clearest clues to its long gestation. Speech itself involves over 100 muscles and complex anatomical structures that require coordination and planning at the ten-milliseconds and millimeter scales, and the evolution of specialized neural connections to the tongue, the larynx and the intercostal muscles, the extension of the arcuate fasciculus and the development of other neural circuits (e.g. [74]). A deep prehistory to language seems inevitable, especially as the new analyses of early AMH fossils in Morocco already double the time depth of our own lineage [3*,40*], and part of this prehistory may be traceable in the interactional infrastructure for language which includes the sustained mutual attention and the exchange of turns at production, infrastructure which is probably phylogenetically deep among the primates [75].

Language seems to be a precondition for the transmission of elaborate lithic technologies: novices were systematically taught [65] the simple *Oldowan* technology under five different conditions (reverse engineering, emulation, basic teaching, gestural teaching and spoken teaching) and found that full linguistic teaching led to the most efficient technique and good tools, followed by gestural teaching. The reasons are that efficient knapping relies on not easily observable skills, like knowledge about platform angles just under 90 degrees. If one considers all of the cultural skills needed to survive in ecologies from the Arctic to game-poor Mediterranean littorals, it is difficult to argue that Neanderthals lacked complex linguistic codes, capable of communicating about spatial locations, hunting and gathering, fauna and flora, social relations, technologies, and so on. This would imply a large lexicon, and propositional encoding. Granting Neanderthals advanced language capacities seems to us inevitable.

Conflict of interest statement

Nothing declared.

Acknowledgements

We wish to thank Ludy Cilissen for help with drawing the figure, Cedric Boeckx and Didier Demolin for discussion, and William Marslen-Wilson for comments on an earlier draft. DD was funded by the NWO VIDI Grant No. 276-70-022 and an EURIAS Grant 2017–2018.

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