



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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Introduction

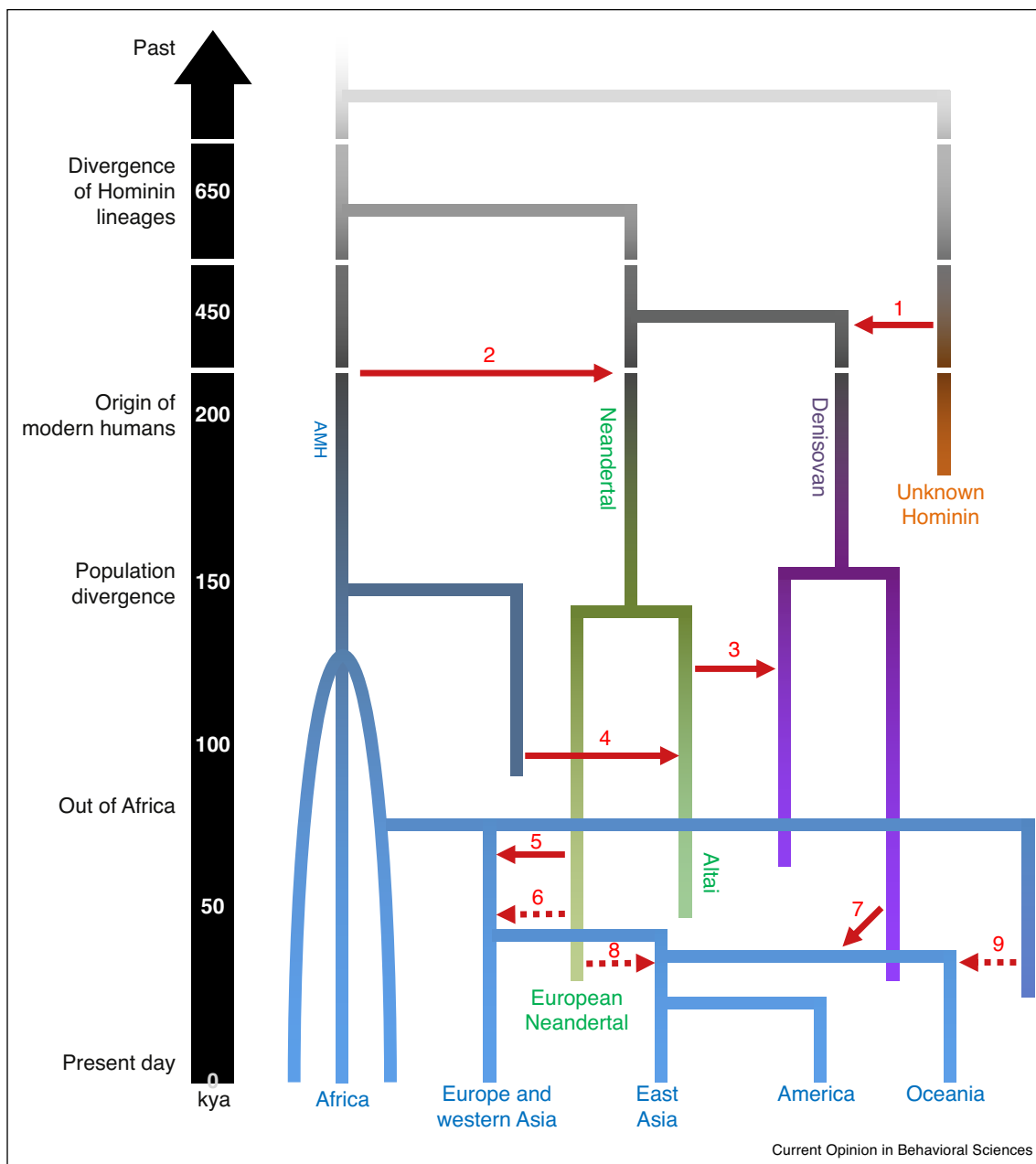
In 2013 we published a paper [1] arguing that vocal language has had a long and gradual evolution in the 1.5 my since *Homo erectus*, and that Neanderthals were articulate humans, not very different from us. We marshaled paleontological, archeological and genetic evidence against the saltationist view 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 Atai 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

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