

Archaic human genomes and language evolution

John Hawks

Department of Anthropology, University of Wisconsin-Madison, Madison, WI 53706, USA
e-mail: jhawks@wisc.edu

Strongly divergent groups of Middle Pleistocene peoples, including Neandertals, Denisovans, and multiple groups of sub-Saharan Africans appear to have contributed some of the genetic ancestry of human populations today (Green *et al.*, 2010; Reich *et al.*, 2010; Hammer *et al.*, 2011; Lachance *et al.*, 2012). Could these different groups of archaic hominins talk and comprehend spoken language like recent humans? Benítez-Burraco & Barceló-Coblijn (this Forum) argue that these archaic humans probably lacked some of the defining features of modern human language, and that the genetic mixture of these populations probably did not prompt the emergence of language in modern humans.

On purely genetic grounds, the evidence remains insufficient to refute this hypothesis. The coding sequence of FOXP2 is shared among modern, Neandertal, and Denisovan genomes (Krause *et al.*, 2007; Meyer *et al.*, 2013) but at least one proposed regulatory mutation separates most living humans from chimpanzees; the known Denisovan and Neandertal genomes lack this change (Maricic *et al.*, 2012). Still, this genetic mutation is not today fixed in human populations. Many people today live normal lives without this new variant “modern” regulatory variant. This is one example in which the functional importance of the variation present in living people remains unclear.

Indeed, this single example is concordant with the overall pattern of variability within human genomes and ancient genomes. Humans today are much more genetically similar to each other than any living person is to a Neandertal or Denisovan. Even so, there are strikingly few

genetic changes in humans that are fixed differences between all known living humans and Neandertals and Denisovans. Mostly, a small number of people still retain ancestral alleles shared with Neandertals, Denisovans and probably many ancient African peoples. From the point of view of inheritance and genealogy, we assign some importance to Neandertal ancestry. But from the point of view of function, it does not matter whether living people inherited an allele from Neandertals or from our shared African ancestors, if it has the same functional effect. The number of new coding substitutions shared by all known humans and not present in Neandertals is fewer than a hundred across the whole exome (Burbano *et al.*, 2010). The number of new regulatory non-coding variants fixed in humans versus Neandertals and Denisovans is not yet known, but is likely of the same order of magnitude.

This pattern of variation may be a tremendous advantage as we move to test hypotheses about the language phenotype of Neandertals. Almost all Neandertal and Denisovan coding alleles occur today in some small fraction of living people. If some of those alleles were important to functional aspects of cognition or language, a comparison of living people who carry these alleles should show their importance.

The record of behavior genetics shows us that the effect of any single allele on the variation within human populations is likely to be very small. Performance on psychometric tests measuring cognitive performance, for example, is often moderately heritable as assessed by traditional pedigree-based methods such as twin or sibling studies. But genome-wide association

approaches have shown no very common alleles of strong effect, and so far explain only a tiny fraction of the heritability of test performance (e.g., Davis *et al.*, 2010). Suppose that the genetic network underlying the evolution of language likewise involved many genes of small effect and very rare large-effect genes. In this model, we would need to examine large numbers of alleles shared with Neandertal and Denisovan genomes to test the hypothesis that these ancient populations had different language abilities than living people.

Many anthropologists once hypothesized that the “human revolution” of art and ornamentation is a marker of the first appearance of language. We now appreciate that art and ornamentation emerged more gradually across the Middle to Late Pleistocene, in both Africans and Neandertals (d’Errico, 2003). The level of cooperativeness and coordination in early *Homo* must have required some language-like communication, if not modern language (Schepartz, 1993). Certainly, the vocal-auditory channel seems to have undergone selection in early *Homo*, presumably for use in communication (Martinez *et al.*, 2008). Still, some linguists and anthropologists still assert that human language appeared suddenly and recently in our evolutionary history (Berwick *et al.*, 2013). The idea of a recent appearance of human language appears to contradict the signs of a deeper record of vocal communication.

We can resolve this contradiction by moving past the analogy of a “linguistic genotype” shared by all living humans. In most instances of recent human adaptation, we see widespread convergence of human genetic changes. Classic cases include malaria adaptation, pigmentation, lactase persistence, and high altitude adaptation, among many, many others. In each of these examples, a common selective pressure in different human populations has led to similar phenotypic responses based on different genetic changes. Thousands of years of strong selection on these phenotypes has not eliminated the alleles that characterized pre-Holocene peoples; those alleles remain in human populations and we continue to discover their effects.

As Pinker & Bloom (1990) pointed out, the selective advantage of an allele that reinforces a learned behavioral trait actually declines as the allele approaches fixation. This is because the probability that an individual will fail to learn the behavior declines to zero, eliminating the additive variance of the behavioral trait. Selection on learning more difficult elements of the behavior may remain strong even while genetic variation remains to characterize more easily learned elements. Language is an exquisitely complex behavioral system; its genetic evolution should have matched this complexity.

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