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Also sprach Neanderthalis… Or Did She?

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1. Introduction

Two Neanderthals from El Sidrón (Asturias, Spain; Rosas *et al.* 2006) have been recently analyzed by Krause *et al.* (henceforth K) for possible mutations in *FOXP2* (Krause *et al.* 2007), a gene involved in the faculty of language (Lai *et al.* 2001). Although these mutations were believed to be specific to modern humans (Enard *et al.* 2002), this investigation revealed otherwise. Other details of the genomic analysis of these specimens led K to the conclusion that "these two amino acid substitutions […] associated with the emergence of fully modern language ability" (Krause *et al.* 2007: 1908) were probably inherited both by Neanderthals and modern Sapiens from their last common ancestor (300,000 to 400,000 years B.P.).[1]

We argue that the data offered by K are compatible with less drastic interpretations, which we consider in three successive scenarios: (1) the mutations could be selected in Neanderthal's genetic endowment, but for some non-linguistic function; (2) they could be present, but unselected; or (3) they could be transferred into Neanderthals from modern humans through gene flow. Thus K's analysis does not confirm either the antiquity of the human faculty of language or the linguistic capabilities of Neanderthals, and more reliable data are still needed to settle this intriguing question.

The main conclusion that we have reached after discussing this paper is that K's data do not discard the idea that the faculty of language is an evolutionary innovation specific to anatomically modern humans. In fact, such a possibility is now supported by a recent study by Coop *et al.* (2008), and continues to be the most congenial with the behavioral asymmetry between Neanderthals and modern humans that the fossil record reflects (Klein with Edgar 2002: ch. 6, Mellars 2005, and Mithen 2006a). Whatever the origin for the mutations under discussion, they do not entail that Neanderthals from the

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1 The amino acid substitutions under discussion are caused by nucleotide substitutions at positions 911 and 977 in exon 7 of the *FOXP2* gene, which change threonine to aspartic acid and arginine to serine residues, respectively.

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relevant populations were capable of speaking in a modern way. This is quite simply because although *FOXP2* is arguably a necessary condition for language, it almost certainly is not a sufficient one, by any stretch of the imagination. Indeed, for this very reason any corroboration of K's analysis about the antiquity of the mutations in question would not entail that a modern faculty of language was accessible to humans before the evolutionary split leading to Neanderthals.

2. First Scenario

K claim that the selective sweep on the evolutionary changes of *FOXP2* started before the split of the ancestral populations of Neanderthals and modern humans, some 300,000-400,000 years B.P. They also contend that the fixation of these mutations occurred within the last 260,000 years and were completed by 180,000 years B.P.

Based on an analysis of intronic regions (including the one investigated by K), a previous study by an overlapping team concluded that the modern mutations in *FOXP2* took place within the last 200,000 years, most probably around 125,000 years B.P. — thus concomitant with or subsequent to the emergence of modern humans (Enard *et al.* 2002).[2] K would do well to clarify in detail how their conclusions harmonize with the population reasoning offered in that earlier study.

That said, prospects other than Neanderthals having a complex human-like faculty of language are compatible with K's favored scenario. They themselves emphasize that uncertainties in *FOXP2*'s function in Neanderthals could only be cleared by a more complete sequence of the gene, which might uncover some further Neanderthal-specific substitutions. We agree with the skepticism this invites with regards to the putative existence of a complex form of language among Neanderthals, but our reasons are quite different.

A high degree of conservation of *FOXP2* orthologues among vertebrates has been independently established (Enard *et al.* 2002), which makes the existence of more substitutions within the complete sequence of the gene in Neanderthals rather improbable. However, the key to settle this question is not so much the complete sequence of *FOXP2* in Neanderthals, but attaining more information about the genetic context in which the gene displayed its regulatory function in this species. Unfortunately, this kind of information is rather sparse even in the case of modern humans (Spiteri *et al.* 2007, Vernes *et al.* 2007) and of course is completely non-existent in the case of Neanderthals.

Modern *FOXP2* could have become fixed in Neanderthals for reasons different from those operating in modern humans. Within a different genetic context, it could have helped regulate the development/execution of a symbolic but non-syntactic proto-language (Bickerton 1990), or some other form of quasi musical vocalizations (Mithen 2006b), among other conceivable possibilities. In

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[2] Coop *et al.* (2008: 1257) assert that the antiquity of the haplotype could be reduced up to 42,000 years B.P. using a different statistical procedure ('phylogenetic dating'). However, as they also alert that "there is considerable uncertainty associated with this estimate", we prefer not to make any statement based on this date.

fact, even identical mutant versions of *FOXP2* can correlate with different acoustic/prosodic phenotypes in the case of modern humans (Shriberg *et al.* 2006). Technically, this idea presupposes the existence of two parallel selective processes with identical molecular outcomes in two different species. It is difficult to assess the probability of such a scenario, but it may be a feasible one considering the genetic, anatomic and physiologic closeness of the two species, as well as the similar selective pressures they could be going through at a certain point of their evolutionary history.

Also relevant with regard to this idea is the fact that different *FOXP2* orthologues have been described for some species and associated with a distinctive ability in each case (see Haesler *et al.* 2004 and Haesler *et al.* 2007 on bird song, and Shu *et al.* 2005 and Fujita *et al.* 2008 on ultrasonic vocalization in mice). But it is worth reiterating again the high degree of conservation of this gene (Enard *et al.* 2002), which has undergone very few evolutionary changes among vertebrates.[3] Thus, in all likelihood the ability with which each *FOXP2* orthologue relates in each species is a function of the molecular context which the protein coded by the gene integrates in each particular case, and not of minor structural modifications experienced by its different variants.

Much more information is thus needed regarding the regulatory networks in which *FOXP2* is involved, and about its target genes in human development, before strong functional homologies in Neanderthals can be explored so that the 'Neanderthal language' question can be properly assessed from a paleogenetic point of view.

3. Second Scenario

The relevant *FOXP2* haplotype could be present in the ancestral populations of Neanderthals and modern humans, but only positively selected in the latter. K reject this possibility because they detect a signal of selective sweep on the Neanderthal region under discussion.

The intronic region located in position 5 from the exon containing the modern mutations of *FOXP2* has been affected by a selective sweep. This is reflected in the low frequency of variants within different modern human populations, in a region otherwise subject to the frequency rates of a standard neutral mutation model. K observe that the analysis of some nucleotids from the same intronic regions of the El Sidrón specimens shows a high degree of identity with the predominant allele among humans. From this they conclude that the selective sweep on the region can be traced back to our last common ancestor with Neanderthals, around 260,000 years B.P.

However, it is important to note that the fact that two Neanderthal variants of the intronic region under discussion are similar to the modern allele does not necessarily entail that all Neanderthal variation concentrate on the same modern-

[3] An exception seems to be the case of some species of echolocating bats, which present massive variants of *FOXP2*. Li *et al.* (2007), who relate the gene with a function in sensorimotor coordination, argue that this fact is to be explained by the divergent selective pressures these species have been subjected to in the evolution of echolocation.

like allele. Thus the signal of the selective sweep on Neanderthal *FOXP2* will only be confirmed by the analysis of a representative sample of individuals of this species.

Furthermore, Coop *et al.* (2008: 1257) argue that the following lines of evidence rule out the possibility of such an early selective process:

> (1) The persistence of ancestral alleles for close to 300,000 years in both Neanderthal and human lineages is unlikely, given that low frequency variants will tend to be rapidly lost from the population by genetic drift. Actually, ancestral alleles among modern humans are found in the intronic region under examination, as well as the ancestral allele in some intronic markers of the Neanderthal sample ; and
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> (2) If the selective sweep was close to completion 300,000 years ago, the selected haplotype should have accumulated more mutations since. Actually, what is noticeable is the scarcity of divergences added up to the haplotype.

If Coop *et al.*'s conclusion is on the right track, how could one explain that the mutations under discussion are present in the genetic pools of both Neanderthals and modern humans but only selected in the latter species? The key to answer this question may be that modifications on the concerted action of *FOXP2* with other genes, in the development of an innovative cognitive structure (Piattelli–Palmarini & Uriagereka 2005), could underlie the selective sweep on the modern mutations of this regulatory gene (Lai *et al.* 2001). Selection operating on a complete module of coordinated genes (Oldham *et al.* 2006, Spiteri *et al.* 2007) in modern humans, but not in Neanderthals, could in principle co-exist with a lack of selective sweep on *FOXP2* in the latter species, even if the modern mutations are relevantly confirmed.

4. Third Scenario

Gene flow could be the source of the two evolutionary changes in *FOXP2* that Neanderthals from El Sidrón share with modern humans. K reject this possibility on the basis of previous analyses of Neanderthal mtDNA (Krings *et al.* 1997, Krings *et al.* 1999, Hofreiter *et al.* 2001, Serre *et al.* 2004) plus their own analysis of the Y chromosomes in the two specimens from El Sidrón.

We are aware that the admixture thesis has been controversial ever since its proposal by Green *et al.* (2006).[4] Nevertheless, it is in principle possible that this state-of-affairs did take place, an thus we should consider the possibility, remote as it may be, of a scenario along these lines for the mutations that concern us here.[5] Actually, this is the preferred scenario of Coop *et al.*, who conclude that K's

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4 See Noonan *et al.* (2006), and Wall & Kim (2007) for a useful comparison between the two theses.

5 Regarding K's arguments against admixture, we would like to briefly note the following facts:

(1) Maternally inherited mtDNA cannot settle the question, as Neanderthal mitochondrial

results "may reflect gene flow between modern human and Neanderthal populations" (Coop *et al.* 2008: 1257).

It is true that the antiquity of the specimens from El Sidrón (around 43,000 years old) is at the limit for such a possibility. In order to shed light on this question, more analysis of specimens from different locations seems imperative, ideally earlier ones than those found in El Sidrón (in the 46,000–50,000 B.P. range or older, taking this as the approximate date of arrival of modern humans to Europe; Oppenheimer 2003).

5. Conclusion

The significance of K's finding cannot be overemphasized. However, even though they are not equally probable, none of the three scenarios commented on here, attempting to explicate such an important discovery, can be summarily discarded. Therefore, we consider that the interpretation of the facts advanced by this team is premature. Many questions still await an answer, and crucial data need to be uncovered, before anyone can assert whether Neanderthals spoke or not.

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haplotypes would be left unchanged by a modern-males-to-Neanderthal-females genetic channel (actually, Green *et al.* 2006 contend that gene flow must have predominantly stemmed from modern human males); and

(2) The analysis of Y chromosome fragments in the El Sidrón specimens is not conclusive in this regard. Clear results have been obtained from only one specimen, and are not identical in each of the laboratories the team worked with (Krause *et al.* 2007, Supplemental Data). While the outcome of the analysis does suggest that no derived alleles exist in the Y chromosome of that one specimen, the possibility cannot be excluded with such sparse data.

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