

Hominin interbreeding and language evolution: fine-tuning the details

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Commentaries on our target paper ‘Paleogenomics, hominin interbreeding and language evolution’ generally agree with (and in some cases support) our claim that hominin interbreeding did not play a crucial role in the emergence of modern language. Several aspects that were not properly attended to in our contribution were also noted. We will try to respond to these here. At the same time our commentators have posited some other important issues that go far beyond our genetic concerns. Such observations are relevant to the discussion about when and how modern language evolved in our clade. We will also try to define our position regarding these questions. After this fruitful exchange we still think that current data do not support the existence of a full-fledged language for Neanderthals. Of course, future findings may show the opposite. One should not be dogmatic about this. The study of language evolution is an intricate enterprise given the evident lack of evidence of Paleolithic languages or proto-languages. In addition, because of the history of this subfield, banned for an infamous period by many academics due to the simplicity for creating just-so-stories, caution is in order. As posited in this debate by Emiliano Bruner, in order to not fall in the same trap, only probable (but not just possible) hypotheses should be considered. We regard our position as probable on the basis of the available evidence. We would like to thank our commentators for their correspondence and also the editor for the possibility of being involved in it.

Bruner: approaching the evolution of the language faculty

Emiliano Bruner has cleverly subtitled his piece ‘Too many answers for too few questions’. We agree with the main point he makes, which is that the field of language evolution must (and actually can, we think) move from the realm of plausible hypotheses into the territory of probable hypotheses. We agree as well with his claim that when current theories about language evolution are subject to falsification, not many pertinent questions remain. However, we also feel that one of these surviving questions is when and how did a full-fledged language appear in our clade. At present we are in position to try to answer this question by putting together all the archaeological, paleo-neurobiological, genetic, and even molecular data available to date. A second key concern raised by Bruner is that we must rely on all evidences if we intend to reach hypotheses that are probable (and eventually, to be able to falsify them). Importantly, it can happen that while looking for the definitive piece that transformed a putative (if any) hominin protolanguage into a full-fledged language, one is probably misunderstanding how evolution proceeds. Modern language probably resulted from the interplay of many components otherwise evolved to fulfil different functions (whether related to language or not). In addition, some properties of language are emergent by nature (see Deacon, 2005). This situation is related to the ‘compatibility’ problem

also raised by Bruner. This concerns the fact that much physical and even behavioural evidence (genes, body organs, brain architecture, etc.) cannot be unequivocally related to modern functions. This is also known as the ‘form-function problem’ (Balari *et al.*, 2013). As a consequence, “such potentiality leaves many doors open, and opposite conclusions cannot be discarded”. This is why we claim that one of the fundamental concerns for language evolution studies should be the question of establishing when all the elements making up language became functionally interconnected. Given the ancillary nature of some language-related features, the question of when the different pieces appeared individually does not seem to be so important. In his commentary Bruner has proficiently discussed the detrimental consequences of this kind of reductionism.

We would like to qualify only one of the statements posited by Bruner; the claim that because “language is one of the most complex human cognitive processes, and it is strictly linked to all human cultural aspects [...] it is likely that culture itself may be the most informative witness of language evolution, more than genes, bones, or circumvolutions”. Bruner’s statement about complexity is correct. As we discuss below, complexity has been observed in both the language faculty and in language as a public code. We also agree that many aspects of language have resulted from cultural evolution. In fact, this can be the case even of core structural components of language, particularly those aspects related to morpho-phonology (see Boeckx, 2013). Nonetheless, we still think that a great deal of evidence supports the claim that some biological change(s) prompted the emergence of the language-ready brain. This label refers only to the component of our biological endowment that allows us to instinctively develop abstract rules that are used for thinking and communication (see Boeckx, 2013 for a comprehensive explanation of this). Among other factors, we need to take into account the way in which the language faculty develops in the child. The results suggest that ‘developing’ a language is a process which is constrained or biased in specific ways. Moreover,

the existence of developmental language disorders is suggestive of the presence of different genes involved in the development of the brain areas that process language. For us, the morphological and ontogenetic – and presumably, functional – differences observed at the brain level between anatomically-modern humans (henceforth, AMHs) and extinct hominins (specifically, Neanderthals), attested to by Gunz and collaborators (2010, 2012) support this view. Of course, this does not entail that this biological change (or changes) was only genetic by nature. As development is regulated by many different factors, all being equally necessary for the final phenotype to emerge, evolution can be prompted by the modification of any of them (Oyama *et al.*, 2001; Griffiths & Gray, 2004).

Hawks: on genetic diversity and developmental processes

John Hawks has examined the biological plausibility of our position under the light of current genetic evidence, leaving in the second place other evidence that can be used for supporting (or rejecting) the existence of a full-fledged language faculty in other hominins. In doing so, Hawks has primarily considered the established differences between the AMH and Neanderthal/Denisovan genomes, and also the either observed or inferred degree of variation at the genomic level among these populations. He concludes that i) the amount of fixed changes in AMHs is expected to be very small; ii) AMH populations are expected to share different ancestral alleles with Neanderthals and/or Denisovans; and iii) it is improbable that any specific allele (either fixed or shared) strongly affects cognition (as studies of modern populations show). We agree that it is not possible to solve this evolutionary conundrum by only genetic means, at the very least because of the role played by genes in development. In fact, we also made use of other, non-genetic evidence to reinforce our claim that Neanderthals lacked modern language. In this context, Hawks alludes to the dispute around the continuity or discontinuity of

human language. In a nutshell, behavioural evidence (e.g. cooperativeness) and the fossil record (e.g. vocal behaviour) point to a long evolutionary history. Nevertheless, some scholars still claim that language appeared suddenly (e.g. Berwick, 2013). Hawks suggests that this contradiction may be solved (or perhaps reconciled) by purely genetic arguments. Hence, AMH populations are endowed with different genotypes but most human features (language included) are shared by all human beings because of common selective pressures. Accordingly, it could be the case that Denisovan, Neanderthal and AMH genomes did not actually differ in important positions (i.e. any genetic modification prompted the emergence of modern language), but that a full-fledged language is still an AMH innovation because of some specific selective pressure on AMH populations.

These are very important issues and we would like to state our own position. Concerning the extant (and presumed) differences between AMHs and Neanderthals/Denisovans at the genetic level, our view is the same as that expressed in our reply to Bruner's commentary: the differences between AMHs and Neanderthals at the brain level (both developmentally and in the adulthood) are real. If we also consider the case for nativism in language acquisition, we should expect some changes, either genetic or (more probably) epigenetic, after our split from Neanderthals. Of course, we will be close to an answer when the Neanderthal and the Denisovan genomes are fully sequenced. However, the issue of developmental variation brought about by Hawks makes this apparently simple picture much more complex. After all, a full-covered sequenced genome is not going to be the final answer. Variation actually pervades language at all levels of analysis: genetic, neurobiological, cognitive, and even psycholinguistic. At the same time, we continue to recognize the language faculty as an idiosyncratic component of human cognition. Ontogenetically, we are beginning to identify the diverse factors that enable development to be canalised as it is. It is also significant that the picture depicted by Hawks shows that there were real genetic differences between

extinct hominins and AMHs. However, we cannot assign to any principal gene a causative role. This parallels what we observe in complex genetic diseases. In these conditions we either observe "no very common alleles of strong effect" [and] "many genes of small effect". There are a number of genetic models that account for these diseases (e.g. Becker, 2004; Schork *et al.*, 2009). Even more importantly, an Evo-Devo perspective allows us to productively (and deeply) link both typical and atypical development and evolution. For instance, according to Gibson (2009), complex diseases can be construed as decanalized conditions resulting from the uncovering of cryptic genetic variation prompted by our specific evolutionary history (which includes acute bottlenecks and long-distance migratory movements) but also by some specific mutations and/or cultural changes. This explains why complex diseases are so pervasive and prevalent among modern populations, but also why such diseases are so elusive to analyze genetically. In his piece Hawks argues for "moving past the analogy of a 'linguistic genotype' shared by all living humans". Likewise, we argue for moving past this model of complex diseases. What if modern language is also a sort of decanalised condition? Seen from this perspective, language is easy to disturb because it is an evolutionary novelty, but is equally resistant to certain kind of damage because it also relies on robust cognitive mechanisms with a long evolutionary history (see Benítez-Burraco & Boeckx *in press* for a detailed discussion of this). We feel that this can be an even more productive approach to the puzzle of language evolution (and to the conflict between continuity and discontinuity) than the genetic approach *per se*, because it integrates Evo-Devo theories in language evolution studies.

As it was the case for Bruner's commentary, our last point concerns the complex nature of language also mentioned by Hawks. He is right as well in his characterization of language as a complex system. But we would like to go beyond metaphors and assert that language behaves exactly as other complex systems studied until now by physicists. If we also consider that its development is postnatal and undergoes

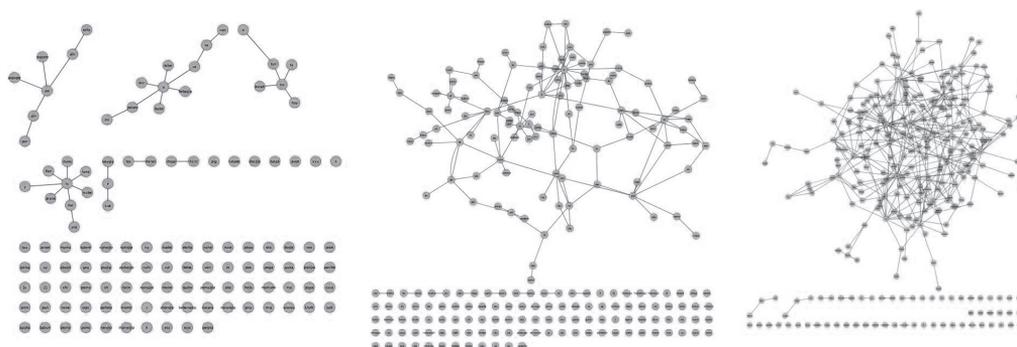


Fig. 1 - Phase transitions in child speech during one whole year of life as a measure of changes in syntactic complexity. The figure is taken from Barceló-Coblijn *et al.* (2012). In this work three corpora (Dutch, German and Spanish) corresponding to one year of life of three children were analysed. From each corpus at least 17 files of transcriptions of single conversations were obtained. Each conversation was syntactically analyzed following the basic lines of Dependency grammar. From each analyzed file a graph was obtained. The figure shows the output of the Spanish-speaking child (corpus Aguirre 'MAG') at three different stages of development (age is represented as "year; months. days"). A graph typically contains several components of one or more nodes. The focus of attention is the Giant Connected Component (GCC), i.e. the largest network in a graph. As it can be noted, the GCC becomes larger as the child grows. Nonetheless, the topology of the network changes as well. On the left, the GCC is a tree-like network. In the middle, the GCC has become a scale-free network. On the right, the scale-free network has gained the feature called 'small-world'. The network is now characterized by a high clustering coefficient and a low path length.

a non-linear process (Ninio, 2005; Corominas-Murtra *et al.*, 2009), the consideration of the possibility of different linguistic phenotypes (see Balari & Lorenzo, 2013 for discussion) is opened up. For example, results of the production of children seen in terms of network analyses show that AMH children undergo some phase transitions (see figure 1). Also, the pattern of complexity extracted from their production changes dramatically at least two times before reaching adult linguistic completeness (Corominas-Murtra *et al.* 2009; Barceló-Coblijn *et al.*, 2012).

Villar & Gomila: minimising the role of genetics

Villar & Gomila also argue for 'a minor role for genetics in language evolution'. We agree with their vindication of a major role of development in language growth and evolution (see above our commentaries to Bruner's and Hawks' reviews). Villar & Gomila examine different

evidences usually employed for inferring linguistic abilities in hominins (symbolism, communication and burials). They conclude that i) "the Neanderthal society [...] was a linguistic community"; ii) "both cognitively and culturally, Neanderthals and AMHs were similar"; and iii) "both species were capable of speech (referring to Barceló-Coblijn, 2011)". Notice, however, that they also conclude that "such a complex form of language [i.e. hierarchically structured] was made possible *by some genetic change, linked to the appearance of our species*" (emphasis added). In other words, that only AMHs have a full-fledged faculty of language. They base their conclusions on i) the observed differences in developmental trajectories between both species, as attested by Gunz and collaborators (2010, 2012) (though this was in fact our point), and ii) the proposal by Camps & Uriagereka (2006) on knots as a proxy for syntactic abilities. Note however that, if all this was brought about "by some genetic change", the role of genetics in language evolution is not going to be that minor.

Villar & Gomila's criticism is mostly directed against the label 'linguistic genotype'. We used this term as a shorthand for the whole set of genes currently related to language – also in the plain sense that their mutation gives rise to language deficits. We do not believe that a linguistic genotype *stricto sensu* actually exists – at least not one which comprises genes exclusively involved in the regulation and growth of brain areas that are specifically related to the components or operations of language. In fact, we have quite extensively written against this view (e.g. Benítez-Burraco & Longa, 2010, 2011). We do believe that language features are not directly rooted in the genome. Instead, we favour the view that a direct link between the genotype and the phenotype is not only simplistic, but biologically untenable, if only due to the way in which genes contribute to developmental processes and to how development actually takes place.

We would also like to address two minor concerns raised by Villar & Gomila. On the one hand, when they review our arguments in favour of a 'late' scenario for the emergence of modern language, they claim "that the 'linguistic genotype' may still be *Sapiens* only, as long as the Neanderthal DNA found in our species is unrelated to language". Significantly, the other view also holds: i.e. fixed changes in genes that are important for language have not been shown to exist in Neanderthals (e.g. *CNTNAP2*, *ASPM*, etc.). On the other hand, with regard to the issue of interbreeding vs. speciation in relation to linguistic abilities, we are also convinced that Neanderthals were capable of socializing with AMHs (and even mating with them) in spite of having a differently structured 'language'. After all, AMHs are also able to do the same with their conspecifics by relying on pidginised (i.e. structurally simplified, functionally reduced) forms of language. Importantly, this is not to mean that Neanderthal 'language' was like extant human pidgins: behind a pidgin there is always an AMH brain (and this was not probably the case even with the hybrids between both species). Also, a pidgin is never entirely independent from the influence of a full-fledged language. On a different note, reproductive isolation is by no

means the only hallmark of speciation. Also, geographical and/or behavioural isolation can bring about separate species (even if they are able to produce fertile hybrids when they eventually interbreed). In fact, this could have been the case with Neanderthals and AMHs. In other words, both groups were geographically and behaviourally isolated for most of the time, in spite of being cross-fertile. The fact that the different environmental conditions in which they evolved probably pushed their developmental trajectories in different directions is another important point to be considered. Finally, we would like to stress that genetic introgression is not uncommon within mammals (Mallet, 2005; 2008). At the same time, it does not preclude nor favour a particular phenotype per se. A lesson learned from the Evo-Devo perspective is that there is much room for individual differences during development, and that sometimes there are individual deviations from the typical development of a group (Alberch, 1989; West-Eberhard, 2003).

Broadening the debate: Rosas, Premo, Di Vincenzo & Manzi and Ferretti

On the whole, the contributions by Antonio Rosas, Luke Premo, Fabio Di Vincenzo & Giorgio Manzi, and Francesco Ferretti acknowledge in general the correctness of our analysis and the plausibility of our position and in some cases even recognize that extinct hominins were probably not endowed with complex language. However, these authors focus instead on the broader question of the linguistic abilities of these species and the nature of the evidence on which we can rely to confidently infer them. Although this debate clearly exceeds the scope of our target paper, we would like to define our position regarding it.

Rosas: on speciation and language

Antonio Rosas brings to the fore the interesting question of whether Neanderthals were actually a distinct species. On the one hand, they were

physically different to us. On the other hand, they were behaviourally and culturally (and cognitively?) akin to us. He further posits that language is a key argument within this debate as it is “a kind of hinge between these two extreme sources of evidence [physical and cultural]”.

The possibility that two close hominin species may be cognitively similar, but different with regard to their linguistic abilities depends, quite obviously, on the status assigned to language within cognition. One way is to see thought and language as two different cognitive devices which interact actively in the externalization of thought. Language could be then considered as a filter of thought. A different view of this is expressed by Hinzen (2006) or Gomila (2011), who refuse to accept the alleged filtering role of language, because language intervenes in thought composition. Hence, language is seen as part of the structure of thought. This second position emphasises the intervention of syntax. In fact, Hinzen (2013) has recently made an argument for conflating the Fodorian language of thought (LOT) with narrow syntax. Quite obviously, from this latter viewpoint, linguistic (i.e. syntactic) differences entail cognitive differences. In this sense, Rosas rightly claims that the main objective of our research should be “to untangle their structures and specificities [that of other hominin languages]. Not just classifying them in the one single dimension of “more or less” simple than the ones from present humans”. In fact, it is well known that there are several possible levels of syntactic complexity. Human language is endowed with a syntactic device that falls within the levels of context-sensitive and mild context-sensitive grammars (Chomsky, 1956, 1959). Accordingly, the whole issue of Neanderthal language should (and can) be reappraised to ask whether Neanderthals also had a modern, complex syntax. Importantly, this level is established by our working memory (Coolidge & Wynn, 2005). Hence, the more enhanced working memory (plausibly linked to specific brain changes), the higher the level of complexity achieved by the computational device. This explains the recent interest in searching for proxies of syntactic abilities. One proxy of this kind is the ‘fossil’ evidence

of the enhancement of our working memory (see Balari *et al.*, 2013). Other such proxies include the knots mentioned by Villar & Gomila (bearing in mind that knots are performed manually; consequently, we should assume that the underlying recursive system of computation is used for both motor and linguistic behaviour [more on this below]). In achieving this task of untangling the structures and specificities of other hominin languages, Rosas awards linguists a leading role. After all, they have a lot to say about “the evolutionary structural disparity of hominin languages”. However, according to our view, other forms of expertise (particularly, paleo-neurobiologists and archaeologists) are equally needed.

Concerning the claim that language is something both physical and cultural by nature, we regard it as being correct, in that language development depends on both the biological endowment and the cultural milieu (i.e. linguistic stimuli). However, we think that to suggest that language is just something halfway between both poles, a mixture of nature and culture, is not entirely satisfactory. In our opinion, some specific biological changes first brought about the language-ready-brain, as we claimed earlier. The brain thus became capable of constructing sets of symbols endowed with a hierarchical structure. Afterwards, such (proto?) language was refined, in part by cultural evolution. According to Boeckx (2013), the enhanced, biologically-evolved mechanism of combination reshaped language semantics and phonology. In turn, cultural evolution gave rise to some of the grammatical properties exhibited by current languages, particularly, those related to morpho-phonology. This is not then a black-and-white picture of the problem, but quite a shaded one.

Finally, we would like to remark on the two research lines that, according to Rosas, could potentially help us to “to decipher the differences in internal organization between the same-sized brains of these taxa”. Concerning the comparative anatomy study of brain components, we agree that this line is of outstanding relevance, perhaps not so much because of its connections with social complexity, as Rosas suggests, but

because it helps us to reveal new ways of connecting pieces within the hominin brain. For instance, Boeckx (2013) has argued that the AMH-specific globular braincase is suggestive of a new anatomical configuration and ultimately, of a new neuronal workspace that would account for our species-specific mode of computation – that is, our ability to form potentially unbounded hierarchical structures. With regard to the second of these lines – namely the search for genetic differences affecting speech abilities (probably, via the *FOXP2* network)–, we would consider this as being of less interest, provided that current research suggests that it is essentially related to the externalization of language (e.g. Kurt *et al.*, 2012). Most scholars agree that aspects of language related to externalization are expected to be more complex and varied, and to have a longer evolutionary history. Today we also know that vocalization is an ancient channel for communication, to the extent that most mammals employ it, with some differences in degree. In fact, monkeys use vocalization much more often than the ‘silent apes’, to borrow Snowdown’s (2004) expression. The deeper record of vocal communication ensures that this strategy has long been the preferred one in mammals. That said, speech is not necessarily the hallmark of modern language (after all, sign languages are endowed with the same fundamental properties as oral languages, but are transmitted visually, instead of orally). This fact leads us back to the null theory. As pointed out by Barceló-Coblijn & Benítez-Burraco (2013), the feature that differentiates human language from any other animal communication system is the particular way in which the elements of the signal are ordered (see Hurford, 2011 for an excellent review of syntactic order in non-human animal communication systems).

Premo: on symbolic thought

Luke Prema also seems to have found our arguments convincing. In fact, he ends his piece by claiming that “ancient DNA has the potential

to help in ways that archaeological and human paleontological lines of evidence cannot”. At the same time, he has provided us with some relevant methodological considerations about the differences that exist (or should exist in language evolution studies) between evidence for the presence of language, evidence for the absence of language, and evidence for the potential of language (in the line of Bruner’s general considerations). Add to these the fact that absence of evidence is not evidence of absence.

As he has reviewed some of them, we want to contribute to his examination of “those lines of evidence [that have commonly served] as “proof” of language in Neanderthals”. He firstly considers the case of “artefacts that may have carried symbolic meaning”. According to him, the fundamental question is whether these artefacts can be manufactured and used in the absence of language. He correctly reasons that we need an independent confirmation (i.e. not related to their symbolic nature) of this possibility. This is an important claim, as it entails changing the focus from the symbolic value per se of these proxies. After all, symbolism is not at stake. Symbolism, understood as a purely representationalist cognitive process could conceivably have been similar in Neanderthals to that of AMHs. However, lexical units (i.e. words) go beyond representation, as they contain syntactic cues too (i.e. edge features that command which other units they can merge with). It is this quality that makes them able to be combined. Extinct hominins could well have been symbolic species, in Deacon’s terms (1997), but simultaneously lacked modern language. As we have already claimed, the hallmark of modern language is the specific way in which symbols are combined. In relation to this issue, Prema mentions Tomasello’s position of it being unlikely that a highly effective transmission of sophisticated techniques can be achieved via a less structurally complex (i.e. not fully syntactic) language. Once again, pidgins are probably good counter-examples. They are not necessarily the best tool for metalinguistic reflection or for poetic play, but they transmit information in fairly effective ways. Consequently, it may

be insufficient to only focus on better ways of identifying cumulative culture in the Paleolithic record, if this cumulative culture can be eventually supported by a less complex language. At the same time, some informative relationships between language and cumulative culture may actually exist. This link has been differently, but quite productively explored in the context of the evolution of the working memory (Wynn & Coolidge, 2004). As we have pointed out before, this can be a key step in the evolution of the computational system of language (see Balari *et al.*, 2013 for a detailed discussion).

Di Vincenzo & Manzi: the motor-language connection

The contribution by Fabio Di Vincenzo & Giorgio Manzi is a fairly long and well supported discussion on the relevance of social learning to the evolution of language. According to the authors, language evolved as a result of changes in sociality, diet, technology, and brain expansion that were fuelled by new ecological conditions. Di Vincenzo & Manzi place special attention on the issue of technological change in the human lineage and on the social transmission of the involved know-how. In doing so they go beyond Premo's position and explicitly argue for a computational approach to the problem that focuses on the procedural system required for planning and executing the involved motor behaviour. In essence, they make a claim for "the co-evolution of motor praxis and sound-coding". According to the authors this possibility is supported by extant paleoneurobiological evidence. As they present it, this is a full-fledged theory sustained with ample (paleo)neurobiological data, but in our opinion it unfolds a parallel scenario that does not actually dispute ours. However, we will be commenting on a few aspects that we see as being debatable.

Firstly, we find the suggested evolutionary link between motor activities and speech (especially via the *FOXP2* network) to be appealing (and convincing). As we pointed out above the

possibility that the *FOXP2* interactome is primarily related to the externalization of language (i.e. the learning of vocalization) is widely recognised and supported by ample comparative evidence (e.g. Kurt *et al.*, 2012; Boeckx, 2013). At the same time it is important not to conflate speech and the language faculty. As we also pointed out in our commentary to Rosas's piece, speech is just one way of externalising linguistic sequences. A different (although related) possibility is that a central computational device is involved in the planning (and execution) of both motor actions and linguistic sequences, a possibility that we find even more convincing (see also Balari & Lorenzo, 2013). This would involve syntax and motor behaviour evolving from the same computational device. Quite probably, the 'fossil' proxies of this device are easier to find (and to interpret) than the traditional 'fossil' proxies of language *per se* (see Balari *et al.*, 2013 for some candidates). Boeckx (2012, 2013) has argued for an alternative view, according to which modern syntax resulted from a brain reorganizational process not linked to new mutations on *FOXP2*, but on some gene(s) controlling the development of the thalamus (see Boeckx & Benítez-Burraco, submitted, for details). However, the attested comorbidity between motor and language disorders in AMH populations is still an important piece of evidence supporting the 'central device hypothesis': whenever one of the brain areas comprising this central device is affected, both motor and linguistic disturbances simultaneously appear in the subject. For instance, patients suffering from Huntington's disease usually exhibit linguistic and motor problems (Teichmann *et al.* 2005; Robins Wahlin *et al.* 2010). This condition is caused by the selective atrophy of the basal ganglia, one of the subcortical components of the computational system of language (see Ullman, 2001; Lieberman, 2002). Similarly, dyslexics sometimes show drawing deficits (Eden *et al.*, 2003; Lipowska *et al.*, 2011). It has been hypothesised that this comorbidity is caused by the impairment of the rule abstraction mechanism inherent to sequential learning (Vicari *et al.*, 2005; Pavlidou *et al.*, 2010).

In any case, what we find unclear or even contradictory in Di Vincenzo & Manzi is the statement that “the presence of the *FOXP2* gene in Neanderthals points not so much to a developed L[anguage] F[aculty] in that species [...] as to the increased selective demand of the upper limbs and mouth motor fine control/coordination *as well as of cognitive computational ability*; thus, it is probably more closely related to mid-Palaeolithic techno-complexes than to a developed LF [emphasis added]”. This is contradictory so long as it seems to conflate speech (i.e. ‘mouth motor fine control’) and the language faculty (which includes ‘cognitive computational ability’), and also to blur the real role played by *FOXP2* in the emergence of modern language (see above). The authors seem to suggest that an enhanced (i.e. recursive) computational system was brought about by modern mutations on *FOXP2* (that are present in both Neanderthals and AMHs). Do they also suggest that this device was initially involved only in motor behaviour (including orofacial movements) and cognitive processing (in both species), and that it was later co-opted for modern syntax in our species only? If this is the case, there are not conclusive evidences of these (enhanced) cognitive computational abilities in Neanderthals. In the same vein, if the authors are suggesting that these mutations brought about an enhanced computational device which was otherwise functionally unspecific (i.e. able to process both motor and cognitive primitives), why did the change only manifest at the speech (i.e. externalization) level? Finally, if the presence of the *FOXP2* gene in Neanderthals points to an enhanced control of the “mouth motor fine control/coordination” (i.e. an enhance speech) “as well as of cognitive computational ability” (i.e. an enhanced syntax), why were Neanderthals endowed after all with an underdeveloped faculty of language? Is it the case that their conceptual abilities were different to ours (quite roughly, language equates to speech plus syntax plus semantics)?

Secondly, with regard to the (paleo)neurobiological evidence reviewed by Di Vincenzo and Manzi, we would like to note that the area 47

(or Broca’s cup) which they refer to is not sufficient to account for language. In fact, Friederici *et al.* (2011) show that this area intervenes, along with area 44, in mathematical recursion. In turn, during linguistic recursion the highest activity is detected in areas 44 and 45. Moreover, the sub-cortical areas are not included in Di Vincenzo & Manzi’s proposal, in spite of being a central component of the computational system of language according to some neurolinguistic models (e.g. Ullman, 2001).

Thirdly, we would like to qualify as well the importance given by Di Vincenzo & Manzi to imitation. At some point of their piece they write that “imitative S[ocial] L[earning] combines – as it does in the LF – two distinct levels of comprehension [(1)] an action level imitation [...] and (2) a programme level imitation (PLI), which ensures the recombination of each motor act (units of meaning) into a new, hierarchically ordered, form of motor behaviour, which is extremely similar to that of the model. Worthy of mention is a similar process that allows language to assemble syntactic structure into sentences”. Nonetheless, more than fifty years of research into language acquisition by children has concluded (certainly, not without controversy) that language is not acquired by imitation (see Lust, 2006 for a discussion). Of course, there are some components of language that are acquired in this way, but this is not the case with the core components of syntax. Putting it simply, the computational system of language is productive by nature. This means that it can generate an unbound set of sentences from a finite set of symbols. Consequently, this behaviour cannot be entirely learned. This conclusion is not directly against Di Vincenzo & Manzi’s position: it only suggests that the recursive and unbound system of computation that AMHs are endowed with must be part of their biology. In other words, for us the crucial point is not so much when and how the skilful mechanism for imitating (and transmitting) the know-how posited by Di Vincenzo & Manzi was achieved, but when and how it gained the capacity of innovation; that is, the capacity for optimizing previous, more

primitive, less efficient know-hows, plausibly by virtually (i.e. mentally) exploring new options. This is precisely what modern, full-fledged syntactic language allows for (Jerison, 1985).

To conclude, we also agree with Di Vincenzo & Manzi's final claim that "what is likely to have played a pivotal role in distinguishing us from our apelike ancestors is not related to any exclusive equipment [...], but rather to the variety of ecological conditions that allowed some features shared by the Anthrozoidea to become more selectively relevant, and *embrace new and more complex functions* [emphasis added]". This fits with the hypothesis of modern language basically resulting from a reorganizational process that brought about complex syntax and put together different, previously evolved pieces. This hypothesis is deeply rooted in the view of language as a cognitive faculty resulting from the interface of different components (cognitive, neural, genetic), otherwise not specifically linguistic (see Hauser *et al.*, 2002; Barceló-Coblijn, 2012; Boeckx, 2012, 2013; Balari & Lorenzo, 2013; Balari *et al.*, 2013, among many others).

Ferretti: cognitive concerns and non-saltational scenarios

The paper by Francesco Ferretti focuses on the broader (and controversial) issue of the evolutionary continuity of human language within hominin cognition (a concern that was also raised by Hawks). He puts our discussion under the umbrella of Chomskyan models of language evolution (and specifically of Chomsky's Universal Grammar). After briefly reviewing some of the evidences usually employed to infer the presence of modern language (essentially, those related to the speech organs and to symbolic behaviour), he concludes that the position in favour of a Neanderthal language can be equally confidently supported (i.e. Neanderthals probably had speech abilities similar to ours; with regards to symbolism, the absence of evidence is not evidence of absence). Furthermore, Ferretti finds untenable the idea that "human

language complies with principles quite different from those found in any other form of communication" and that it lacks any "form of relationship with the communication systems that have preceded it". Consequently, he argues against a saltational view of language evolution and in favour of a "Darwinian, gradualistic, and continuistic perspective", following Corballis (2011). In a nutshell, according to his proposal speech is a human innovation, but "gestural language can be extended to other hominins well beyond the Neanderthals". Moreover, language processing devices (i.e. syntax) are an exaptation of some preexisting cognitive system(s), to the extent that the study of language evolution should conflate with the analysis of the evolution of cognitive systems.

We would like to first note that the "explicit issue" (in Ferretti's terms) of our target paper is not merely the consequences of the discovery of the modern sequence of *FOXP2* in Neanderthals, but the consequences (if any) of the admixture between hominin species for the evolution of human cognition (and language). As already noted by Hawks, the real paradox from a biological perspective is the existence of measurable phenotypic differences between Neanderthals and AMHs (importantly, at the skull/brain level and in behavioural patterns) in spite of their genomes being very similar. We would like to reject as well the impression that we support the view that an innate Universal Grammar actually exists that was first brought about with our species, and eventually, that the whole suite of devices related to modern, full-fledged languages only appeared with AMHs. In our reply to Villar & Gomila we have argued against the view that principles and parameters are directly rooted in the genome and are implemented as such at the brain level (although the UG label was useful in the early period of Generativism, current models of language, even of Chomskyan persuasion, prefer to talk about a biological predisposition to develop language; in other words, modern humans do not share genetically-encoded principles and parameters, but particular developmental patterns that lead to the development of a language faculty).

That said, we would like to briefly define our position regarding the “implicit presuppositions” of our paper, as Ferretti has foregrounded them.

To begin with, we are not as convinced as Ferretti seems to be that in this discussion the real problem lies in the lack of clear terms of comparison. To some extent it is true that different construals of language have brought about different views of language evolution. Traditionally, models of Chomskyan persuasion have focused on the structural aspects of language (i.e. language as an object), dismissing the functions it fulfils. On the contrary, cognitivist models of language evolution have paid more attention to functions (i.e. language as a tool), finding it secondary to care about the structural properties of human sentences. That said, we find necessary (and uncontroversial, we hope) to differentiate between language, language(s), speech and communication (e.g. Barceló-Coblijn & Benítez-Burraco, 2013). In English, where there is no a distinction between the two first terms (contrary to Romance languages [*lange* vs. *langage*, *lingua* vs. *linguaggio*, etc.]) some researchers have coined the expression *language faculty* to denote the first sense of the word. This notion simply expresses the psychological and cognitive aspects that are necessary to generate and put in use the sentences of a particular language (in the second sense of the word). To be honest, we find our own (implicit) definition of language (or of the language faculty) not ideologically-loaded: a cognitive device that allows us to arrange set of symbols in specific ways to convey composite meanings that are put in use for fulfilling different functions (thinking, expressing feelings and emotions, communicating, gossiping, and the like). In the end, both sides of the coin (i.e. structure and function(s)) are relevant with regards to language evolution and are interconnected at a deeper level.

Additionally, we find that the dichotomy gradualism vs. saltationism is misleading when it is not properly construed. Some traits actually show a paced record of changes in the fossil register. But leaps and emergences are not illicit ways of evolution. In truth, not all phenotypic outcomes are possible and smooth transitions between

phenotypes are not either always observed. The reason is found in the very way in which phenotypic spaces are organised and, of course, are brought about (see Alberch, 1989 or McGhee, 2006 among many others). We do believe that some core properties of language, when they are considered from an evolutionary perspective, are not really monolithic entities, to the extent that different stages or grades of complexity can be described. At the same time, this does not entail that any level of complexity can be achieved during evolution. If we focus on syntax (a bone of contention in the field), Chomsky himself (1956, 1959) postulated a limited set of different classes of grammars, that we expect to be differently implemented in different extant or extinct species (see Balari & Lorenzo, 2013 for details).

Finally, and related to this last concern, the modular organization of living beings (at all levels of analysis) makes of reorganizational events an important evolutionary mechanism (*evolvability*), to the extent that phenotypic novelties seem to be largely reorganizational rather than a product of innovative genes (see West-Eberhard, 2003 for discussion). In fact, cognitive abilities like language are very probably cross-modular by nature (Griffiths, 2007). Consequently, we should expect some sort of evolutionary continuity between language and the cognitive/communication systems of other species. We thus find correct Ferretti’s claim against “the idea that human language complies with principles quite different from those found in any other form of communication” or against the view that it lacks “any form of relationship with the communication systems that have preceded it”. Nonetheless, we expect to find continuity at deeper levels of analysis (i.e. regarding its cognitive, neurobiological, and molecular underpinnings). Eventually, it is this circumstance that corroborates (we think) our contention that the AMH language faculty is a phenotypic innovation in spite of showing a detectable evolutionary continuity. The proposals by Balari & Lorenzo (2013) and Boeckx (2013), as we have sketched them above, nicely exemplify this change of focus within the very biolinguistic (i.e. of Chomskyan persuasion) paradigm. Both

of them have tried to empty the Chomskyan faculty of language in the narrow sense (FLN) to the limit (or to attribute as much as possible to the faculty of language in the broad sense [FLB]) to be able to conclude that a full-fledged modern language is a human innovation. In fact, both of them contend that the more evolutionary continuity we find in language, the more plausible such possibility is. For instance, according to Boeckx the only specific feature of human language is an unbounded merge. But this is not construed as a radically new mode of combination (in truth, what is new is the fact that it lacks a domain-specificity). Consequently, we need not to expect that this ability results from some sort of evolutionary miracle, but just from some subtle change in the brain architecture.

Conclusions

In conclusion we feel that our initial view of the role of genetic events in the evolution of modern language has been greatly improved after considering the issues raised by our commentators. Although some controversial points have deserved a closer examination, we have fortunately found an ample common ground for discussion. In our view two important lessons can be learned from this forum. Firstly, it is urgent to move from a strictly geno-centric view of the evolution of the language faculty – being it an important part of human cognition – to an analysis of the evolution of the developmental systems underlying language growth. After all, ontogeny creates phylogeny. Genetic differences (like those emerging from the ongoing research on the genomes of extinct hominins) will be worth considering, of course (in particular, they could account for the emergence of the language-ready brain), but we must also take into account developmental dynamics. Moreover, the time has already come to start characterising language evolution in Evo-Devo terms. We must rely on key Evo-Devo concepts such as canalization, developmental plasticity, robustness, or evolvability (and emergence!) if we really want to

know and to properly explain how modern language evolved. Secondly, the time has also come to attempt to transcend the continuist/discontinuist controversy. Certainly language did not emerge as a whole from the scratch in a single step. Nobody actually claims this today. Most (if not all) components of language have a long evolutionary history. At the same time, some specific innovation(s) also account(s) for it. On the whole, language too seems to be the result of reorganizational processes rather than a product of innovative genes, according to current views of evolution (West-Eberhard, 2003).

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