Lluís Barceló-Coblijn[*]

Evolutionary scenarios for the emergence of recursion[**]

> At some point in the very recent past, maybe about 75.000 years ago,
> an individual in a small group of hominids in East Africa underwent a minor
> mutation that provided the operation Merge.
> (Noam Chomsky, 2008)

1. Introduction

In their influential paper "The Faculty of Language: what is it, who has it, and how did it evolve?" (from now on, HCF, 2002), Hauser, Chomsky and Fitch argued for a multi-component approach to language, with the goal to distinguish these mechanisms that are related to other domains of cognition or forms of communication (included under the rubric of the broad faculty of language, or FLB, such as memory or theory of mind) from those mechanism that are thought to be independent from any other cognitive system and thus specific to human language (narrow faculty of language, or FLN). Among these, recursion was singled out as the core mechanism of FLN, in such a way that it was thought to be the language-specific mechanism that differentiates language from both other human cognitive domains and other communication systems in nonhuman species. In other words, recursion was thought to be unique to language in the same vein that FLN was thought to be unique to humans.

[*]   Group of Human Evolution & Cognition, University of Balearic Islands.

As HCF claimed, this constitutes a clear program of research in language evolution as it is capable of making clear predictions that can be empirically studied. In this paper, we intend to contribute to this program by revising the empirical evidence available regarding the two central questions – whether recursion is unique to humans and whether recursion is unique to language. While there is little doubt that recursion is crucial for language structure, it is not so clear that it is unique to language, given the fact that other human cognitive abilities also seem to involve recursion. In the concluding section of their paper (2002), HCF raised the possibility that recursion is not even unique to humans, arguing that recursion might be present in animals in a domain-specific, modular way (for example in navigation) and that during evolution recursion could have become "penetrable and domain-general," and thus applicable not just to language, but also to all types of domains (for example, numbers).

Of course, these are empirical possibilities that call for a broadening of the "research space" which was drawn in HCF's original paper. In this work, following HCF's suggestion, we purport to review available evidence on the two questions given above: a) whether recursion is human-specific – or whether there is evidence of recursion in other animals and b) whether or not recursion is language specific – or whether it can be found in other human cognitive abilities.

By so doing, we also intend to clarify HCF's program by exploring a variety of possible interpretations of their proposal. In our view, it is clear that HCF's focus on recursion makes a lot of sense from the point of view of the minimalist program. The main novelty of this program is the effort to reduce, as much as possible, the core of the language faculty and displace other linguistic features previously thought to be part of the FLN to the interfaces between the FL and the two systems – the conceptual-intentional system and the articulatory-perceptive system. The fact that the minimalist program in linguistics was not discussed in HCF (2002) and the fact that the minimalist program is not yet completed, can help explain the lack of consistency in the very formulation of HCF's proposal for language evolution. For all these reasons, a proper clarification of the notion of recursion is required in order to take seriously HCF's research program.

This paper is structured as follows: in the first section, we propose an understanding of HCF's proposal that we think makes most sense, as a way out of its conflicting interpretations. The second section reviews studies contending that recursion is also present in nonhuman animals; we demonstrate there that in fact the evidence doesn't give ground to such a conclusion.

Then, in the third section, we consider an evolutionary scenario for recursion that makes it uniquely human, because of its hominid origins, prior to the split of African hominids into *H. neanderthalensis* and *H. sapiens*. Finally, in the fourth section, we consider the possibility that recursion appeared not directly in the context of a faculty of language but in relation to more basic motor skills, such as knotting and netting. Archaeological evidence suggests that *H. sapiens* was clearly capable of knotting and netting activities that may involve recursive patterns. The difficult question that arises at this point is the connection between such recursive abilities and recursion as a component of the faculty of language, which opens up a completely new avenue of possibilities.

1.1. On how to understand the program

In their seminal work, HCF proposed a hypothesis that provoked one of the most intense debates in the last three decades about the origins of language and the language faculty. Through this debate (Fitch *et al*. 2005, Jackendoff & Pinker 2005, Pinker & Jackendoff 2005, among many others), it has become clear that the proposed program is not theoretically straightforward or easy to accept. A great deal depends on how precisely their claim is stated and the additional assumptions one takes for granted. Part of the problem has to do with the lack of precision and consistency in the way the program was formulated; as a matter of fact, in HCF we already find several different definitions of what they call the faculty of language in a narrow sense (FLN), i.e. the components of the language faculty assumed to be language specific, with each definition attributing a different role to recursion in FLN:

> We hypothesize that FLN only includes recursion and is the only uniquely human component of the faculty of language. (2002:1569, abstract)

> We assume … that a key component of FLN is a computational system that generates internal representations and maps them into the sensory-motor interface by the phonological system, and into the conceptual-intentional interface by the (formal) semantic system. … All approaches agree that the core property of FLN is recursion. (2002:1571, col.1)

> In fact, we propose in this hypothesis that FLN comprises only the core computational mechanisms of recursion as they appear

in narrow syntax and the mappings to the interfaces. (2002:1573, col. 2–3)

At minimum, then, FLN includes the capacity of recursion. (2002:1571, col.3)

Some commentators take recursion to be the only component of FLN, while others view it as "one among others." Furthermore, recursion is sometimes presented as a computational mechanism that generates a hierarchical structuring of elements, while at some other points it seems to be inextricably related to the mappings of such elements to the phonological-articulatory and the conceptual-intentional levels of cognitive representation. Thus, the first statement singles out recursion as the only component of FLN, while the fourth one suggests that it is one among many of its features; the second, on its turn, decouples recursion from the mappings which it generates to the interfaces, while the third seems committed to the view that the recursive component is to be characterized by the sort of input-output interface representations to which it applies.

From the point of view of the minimalist program, though, it is clear that the interpretation that makes most sense is the one that views recursion abstractly as a mathematical function that takes units and combines them into hierarchical structures. In fact, this relies on the idea that the operation "merge" is enough to account for all sorts of linguistic structures (Chomsky 2010). From the point of view of the minimalist program, there is a clear sense in which recursion is understood as the one and only computational mechanism that generates expressions that happen to be linguistic because of they involve the two interface systems – the phonological-articulatory and the conceptual-intentional one – onto which this expressions map.[1] The goal that guides the minimalist program is to reduce to a minimum what's thought to be constitutive of syntax, by trying to derive the structural properties of external language from the constraints imposed by the interfaces. To put it in Chomsky's terms, the hypothesis is: "Interfaces + Recursion = Language" (Chomsky 2010). From this point of view, several voices in the debate have understood HCF along minimalist lines:

---

[1]   Notice also that as regards the functional characterization of recursion, it is the linguistics/computer science notion of recursion that matters, not the meta-mathematical understanding of recursion, as Fitch (2010) has clarified. The former notion is the one relevant for hierarchical structures, while in meta-mathematics recursion is treated in a broad sense.

> Hauser *et al.* (2002a), for example, continue to claim that grammatically structured languages are unique to the human species, but suggest that the only component of the human language faculty that is, in fact, uniquely human is the computational mechanism of recursion. (Penn *et al*., 2008)

> A recent proposal (Hauser, Chomsky & Fitch 2002) suggests that the crucial defining property of human language is recursion. (Parker 2006)

> Within this shared FLB is what they call the 'faculty of language in the narrow sense' (FLN), consisting only of recursion. (Stebbins 2007)

There is a source of ambiguity in Chomsky's characterization of the program, depending on how the connection between recursion and the mappings is conceived. Thus, it is possible to view the recursion component in complete abstraction from the lexical elements to which it applies when generating syntactic structures. Then, through the mapping onto the conceptual-intentional interface, these structures are thought to receive a logical form that constrains their propositional content as well as a phonological serialization through the mapping onto the articulatory interface, which allows for their transformation into a sequence of motor patterns. But it is also possible to view the recursive mechanism as intrinsically constituted by the interfaces to which it connects; on this interpretation, recursion is taken to be a constitutively linguistic mechanism.

Thus, the risk of misinterpreting HCF's proposal is high. However, in their response to Jackendoff and Pinker (Fitch, Hauser & Chomsky 2005; henceforth FHC), they offer further clarification by considering the possibility of an organism which could be capable of *recursion* but lack the (same) mappings that humans are taken to use. We take it that this is evidence that the intended understanding of the program is to consider recursion in abstraction, as a computational mechanism which generates hierarchical structures of elements regardless of what is the specific nature of these elements, be they navigational patterns, sounds, musical tones, numbers, or, as we will also consider in section (4.2), manual skills. For the very hypothesis that recursion could have appeared in evolution quite apart from language – a conceivable possibility if the hypothesis that it appeared in fact just for language is to remain a hypothesis – an abstract understanding of recursion has to be taken for granted. Otherwise, the characterization of recursion as unique to language would be question-begging. Henceforth,

this abstract reading of recursion is the one we propose in order to assess whether recursion is "unique to humans, and unique to language." In this way, we will be able to consider whether there is evidence of recursion in some birds calls (Gentner *et al.* 2006) or in our ancestor practices of netting and knotting (Adovasio *et al.* 1997, Adovasio *et al.* 2005). In general, our goal is to confront HCF program with data from other evolutionary study fields and discuss whether it fits into them. Accordingly, the question to be asked from the perspective of cladistics and systematics is whether FLN so conceived constitutes a human autapomorphy (a human only evolutionary change) or a homoplasy (an evolutionary change appearing in parallel in two unrelated species)? It should be further investigated if recursion is language specific or whether we can find evidence of recursion in other cognitive abilities? If the latter is the case, are these cases in some form parasitic on language and linguistic recursion (so that they were made possible by the emergence of language)? Or are they, rather, more basic processes independent of language?

2. Data from comparative studies: homoplasy, apomorphy or autapomorphy?

The comparative perspective has proved to be a very fruitful research procedure. The so-called *habituation-dishabituation*[2] method aims to present some kind of input with human intervention reduced *to a minimum,* so that the participant's output or answer is as natural as possible. In other words, this research method intends to maximally avoid conditioning. Its implementation into evolutionary linguistic studies is useful for testing the idea that most if not all components of human language can be found in other species, above all primates, and for establishing what is unique to *H. sapiens*. Naturally, language is more than just words. It involves structured patterns such as rhythm, or phonology (and hence, phonological categories, which are cognitive entities) – it is furthermore based on the merger of structures and complex thoughts, reflections that we make every day. Keeping this in mind, applying the *habituation-dishabituation* method to the study of such a variety of converging elements made it possible to draw some conclusions about cognition, its evolution, and more specifically about language.

---

[2]   It is also called the "familiarization-discrimination method".

2.1. Cognitive micro-abilities and cognitive cladograms

There are two classic examples of how the comparative approach has proved useful in establishing whether a particular feature is uniquely human or not: rhythmic discrimination and categorical discrimination. The latter was put to test three decades ago, when it turned out that chinchillas are able to categorically distinguish between alveolar plosive consonants, namely [t] and [d] (Kuhl & Miller, 1975). This is also true for the new world primate – the cotton-top tamarin or *Sanguinus oedipus* (Ramus *et al*. 2000).

Regarding rhythmic discrimination, Nazzi *et al*. (2000) showed that American 5-month-old children can distinguish two languages on the basis of a rhythmic class, even when those languages belong to different rhythmic classes. Tincoff *et al*. (2005) have shown that the ability[3] for language discrimination possibly predates our first known *Homo* ancestor – *H. erectus*.[4] In their experiment, cotton-top tamarins could discriminate between languages belonging to different rhythmic classes (e.g. Dutch vs. Japanese). Finally, Toro *et al*. (2003) published similar results regarding the behaviour of common mice (*Mus*). Although both those non-human mammal species had difficulty in discriminating between languages of the same rhythmic class, it became clear that this ability used by modern humans for language was present in a species separated from the hominid ancestors 70–80 millions of years ago (mya). Interestingly enough, however, all three species – humans, mice and tamarins – were unable to discriminate between languages when sentences were presented backwards, which may indicate a possible loss of relevant acoustic information.

In particular, the research into categorical perception necessitates a revision of the assumption that it was a human-specific ability, and hence, something to be accounted for in evolutionary terms within the hominid lineage. In the same vein, we have tried to reconstruct which language-related abilities are present in which species through a cognitive cladogram (Nadal *et al*. 2009), reproduced here as Figure 1 but modified with some new data and new species.

Finally, some general aspects of linguistic morphology have been found in other nonhumans primates. Recent reports suggest that human language affixation could also have evolved before the split of the common ancestor of humans and tamarins (Endress *et al*. 2009). These results increase the

---

[3]   We use the term "micro-ability" or ability because these species have experimentally shown to be capable to do that.

[4]   We here adopt Wood & Collard's (1999) proposal for transferring *H. habilis* and *H. rudolfensis* from the genus *Homo* to the genus *Australopithecus*.

number of general elements that should be regarded as components of FLB and further isolate recursion as something special to human language. Curiously, some months after the publication of this paper, Ouattara, Lemasson & Zuberbühler (2009) published the results of a field study that consisted in observing the alarm call system of Campbell's monkeys that suggest that this species uses an analogue of human morphological suffixation. For reasons of scope, we do not review this issue here, but simply advance our doubts about the supposed "morphemes" found and analyzed by the authors. Neither Campbell's monkey calls nor their supposed morphemes seem to be what linguists call morphemes, that is, cognitive entities which are very well structured and demarcated with regard to lexical semantics, lexical syntax and clear referentiality.[5]
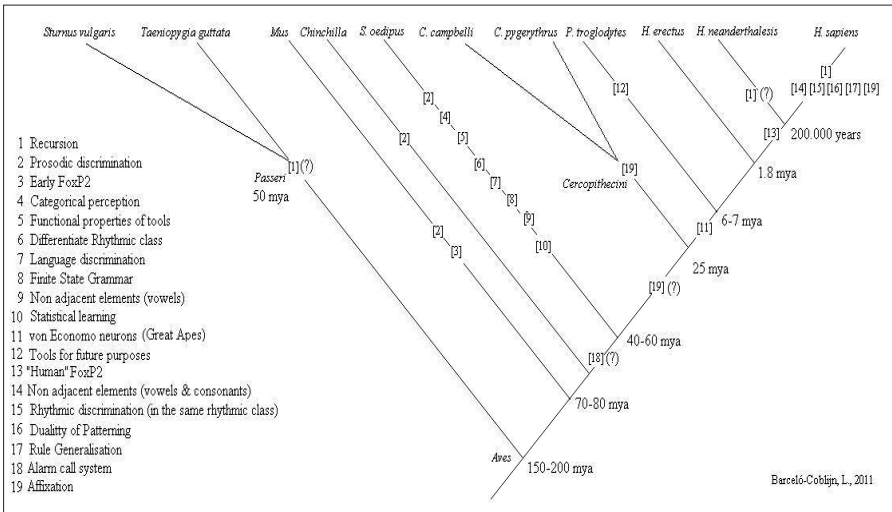

Figure 1. Cognitive cladogram with the attested language-related abilities

We can see that abilities which are today language-related in modern humans can be traced back several mya. Most of them can be roughly divided in three main groups: language perception abilities, language learning abilities and language computational abilities. The last group of abilities is the most interesting for linguists sympathetic to the minimalist program, which seeks to clarify, among other aspects, the computational features that govern linguistic structures viewed as the human cognitive innovations. Note

_____

    [5]   Cf. number 20 in the cognitive cladogram of Figure 1. These doubts have been reflected therein with a question mark, as well as in the case of recursion.

the tentative character of the cladogram: not all species have been put to test for the same abilities and hence, there are still "gaps to be filled".

2.2. Recursion and experimental research

As commented above, for HCF *recursion* is the most important cognitive innovation affecting language. Fitch and Hauser (2004) aimed to test this assumption in an experiment that presented tamarin monkeys with series of sounds with recursive and non-recursive grammars. According to their interpretation, tamarins were unable to process patterns of Phrase Structure Grammars.[6] Due to the fact that Fitch and Hauser's experiment has generally been interpreted as a test for recursion, it triggered off a heated debate about the adequacy of Phrase Structure Grammars, which form the highest level in the Chomsky Hierarchy representing human linguistic capacity (cf. Figure 2, below); arguments against the Phrase Structure Grammar view highlighted the fact that humans scored low in some PSG-related experiments (Coleman *et al*. 2004, van Heijningen *et al*. 2009, Kochanski G., n.d. Liberman 2004, Perruchet & Rey 2005, de Vries *et al*. 2008). However, recent empirical work carried out by Gentner *et al*. (2006) showed very interesting findings challenging HCF's original hypothesis. Namely, if the experiment can be accepted as a test for recursion (*contra* Fitch 2010; cf. Footnote 8), it was observed that, under training, starlings (*Sturnus vulgaris*) were able to process and master species-specific song patterns, which were structured according to the specificities of a Context-Free Grammar. Such grammars belong to the second level of the Chomksy Hierarchy and differ from the first level ones in that they make use of recursion.[7] At this juncture, it should be remembered that according to the traditional vision of computer science and formal language theory,[8] the first level, the so-called Finite State Grammars,

---

[6]   Curiously enough, however, there is one important aspect of this experiment that is not usually commented on, even in linguistics: in some sense, we can say that this experiment was a first implicit attempt to the Pumping lemma test. The adequacy of a grammar to this lemma is what determines whether a grammar is recursive or not. Fitch has repeatedly declared that that experiment was not a test for recursion, contrary to the general interpretation (cf. specifically for this issue Fitch 2010 and footnote 10 in this work).

[7]   Note the inclusion relation the grammars maintain within each other, in a Russian-dolls manner, and how this could induce gradualist arguments regarding the evolution of syntax.

[8]   Fitch (2010: 87) states that "this notion that $A^n B^n$ requires recursion is incorrect,.... In formal language theory, $A^n B^n$ is generally accepted (at least since Chomsky 1957) as a canonical grammar beyond finite-state capabilities, and nothing else. Although one could implement $A^n B^n$ recursively, one can also implement it iteratively without recursion … the (AB)

are *iterative,* not recursive, and hence, computationally less powerful in generating structures.

{{{{Finite State Grammar}Context-Free Grammar}Context-Sensitive Grammar}Phrase Structure Grammar}

    ↑   ↑   ↑   ↑

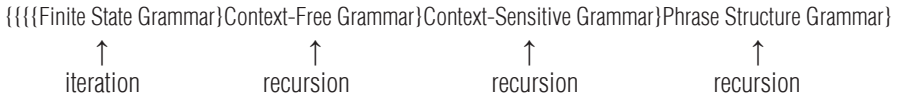 iteration   recursion   recursion   recursion

Figure 2. The Chomsky Hierarchy and the mechanisms that are traditionally linked to its grammars.

Anyway, the discussion about the adequacy of PSG for representing human language is justified since Fitch and Hauser (2004: 378) state that "grammars above FSG level, are, minimally, a crucial component of all human languages." Thus, the debate about which grammar better describes human language is still open to new inquiries.

Given this evidence, a nontrivial question arises: is recursion an apomorphy – a change that appeared in the hominid lineage – or is it instead a homoplasy – a change appeared in parallel in both *H. sapiens* and *Sturnus vulgaris*?

Note that if we understand FLN to be constituted only of recursion – as the most popular version of HCF's hypothesis seems to tell us (cf. Section 1) – one could also think that Gentner *et al.*'s result falsifies such a version of the hypothesis. Nevertheless, even when accepting it, one has to make some caveats before calling HCF's proposal into question. Firstly, in Gentner's *et al.*'s experiment a very different method was followed, since starlings underwent intensive training – which is in stark conflict with the habituation-dishabituation method. Secondly, the kind of stimuli used was markedly different: whereas Fitch and Hauser used human linguistic stimuli, Gentner *et al.* used species-specific sounds. Additionally, a recent paper presented new data on the ability of song birds – specifically zebra finches (*Taeniopygia guttata*) – for processing and mastering recursive patterns, which seem to be at odds with the results of starlings: finches could have just attended to the different order of the elements (van Heijningen *et al.* 2009). Van Heijningen *et al.* argue that the acquired discrimination of zebra finches

---

[n] grammar could also be implemented recursively. … The crucial factor … is that it requires some additional memory mechanism(s) to keep track of "n"". Notwithstanding, if the whole experiment boils down to a memory task, the role of the different types of grammars might be considered irrelevant for non-human animal cognition, according to a more psychological approach.

could be based on phonetic, rather than syntactic, generalization, which can also be applicable to Gentner *et al.*'s experiment.

In this section, we have commented on the most relevant tenets of the habituation-dishabituation method applied to human language research. As we have shown, these studies suggest that some basic micro-abilities – today language-related in humans – could have originated a long time ago, when mammals began speciation and split into several different groups of living beings. But more importantly, they suggest that several of these abilities are unlikely to have evolved "for" language, since all these mammals have no linguistic system comparable to that human language. It is highly doubtful, though, that these "precursors" for language already present in other animals include recursion as a generative mechanism.

3. On population genetics. The spandrel theory

Reconstructions of the Neanderthal vocal tract and other attempts of physiological reconstructions[9] aside, it is clear that recursion cannot fossilize. However, indirect data from other scientific fields might help us to estimate the approximate date of the appearance of such a cognitive trait. Let us review relevant data on evolutionary studies in order to build a bridge between the biolinguistic theory and the paleogenetic and archaeological evidence.

3.1. On the African origins of human cognition

According to mathemathics, there are different kinds of formulas that describe different recursive patterns.[10] Various kinds of recursion have been found in nature, e.g. the well-known Fibonacci series found in the order of the seeds of sunflowers. However, an important difference between this very basic kind of recursion in sunflowers and the kind of recursion argued to be present and functional in human language is – besides their generative power – that linguistic recursion is something that is overwhelmingly active in language. Sunflowers do not create new Fibonacci patterns; rather, the pattern is encoded in their genomes (or is product of the developmental

---

[9]   For the issue of larynx reconstruction and larynx functions, cf. among many others, (Boë *et al.* 2002, de Boer 2007, Fitch & Reby 2001, Fitch 2002, Honda & Tiede 1998, Lieberman 1973, Lieberman & Crelin 1971, Lieberman *et al.* 1969).

[10]   Cf. "Recursive Functions" (Stanford Encyclopedia of Philosophy, n.d).

procces). Instead, humans create new recursive linguistic patterns every time they speak (and *think,* according to proponents of the internalist view). It seems fair to say that wherever recursive linguistic patterns takes place in the human brain, they are the result of some kind of neural interaction. Thus, recursion appears as an active and productive cognitive mechanism. Something has changed in the neural circuitry or functional neuroarchitecture[11] of *H. sapiens* that favors recursive patterning, chaining thoughts in a complex manner, which ultimately might favor the making of complicated calculations, too. But when did it appear in the long history of evolution? In the great apes clade? At some point in the genus *Homo*?

We are convinced of the universal presence of "the recursion mechanism" in *H. sapiens.*[12] As Rebecca Cann and her colleagues showed, it is possible to retrace the distinct human *haplogroups* until their first and unique place of origin in Africa (Cann *et al*. 1983). This and subsequent work in population genetics lent strong support to the so-called *Out-of-Africa* theory, which states that the whole of modern humanity comes from a single place, probably in modern-day Kenya. These studies have received support from the research into the male counterpart, the Y chromosome (Capelli *et al*. 2001, Chiaroni *et al*. 2009, Stumpf & Goldstein 2001). The large – and sometimes rapid, as it seems to be in the case of Polynesia and the Americas – human expansion could have started 200.000 years ago (kya), according to the recent analysis of coalescence made by Kaessmann *et al*. (2001). Their analysis also points out that the DNA sequence variation of *Pan troglodytes* (chimpanzees) is several times greater than that of *H. sapiens*. Thus, the genetic diversity within modern humans is so low that it suggests that there was, from the beginning on, a very small group (probably as the authors suggest, the result of a population bottleneck; realistic models used by the authors imply 3,700 individuals) that suffered a rapid expansion throughout the world. Moreover, if all languages show recursive patterning, this is an indirect parsimonious indicator that probably the first modern human language also showed recursion. The possibility that it later

---

[11]   I here refer both to a possible change in structure as well in function. They are not mutually dependent.

[12]   Its argued absence in Pirahã (Everett 2005) deserves more attention and analysis. In this respect, Fujita claims that it would not be a problem; it could be universal in humans, but some languages might not make use of recursion: "I see no deep conflict between his [Everett's] data and the generativist claim that recursion or embedding is an innate and universal property of human language. In any case, for something to be part of U[universal]G[grammar] it does not require that it be observed in every particular language, extant or extinct". Fujita (2009 141; square brackets added, LBC).

evolved in different – sometimes unconnected – communities all over the world (as homoplasies) seems implausible. Thus, we speculate that a drastic population bottleneck, as Kaesmann *et al.*'s analysis suggests, would have indirectly supported the spread of the recursion mechanism – if it was not yet a common feature present in both Neanderthals and sapiens (cf. Section 4 below).

Altogether this evidence leads us to a preliminary parsimonious scenario: the recursion mechanism – being the fruit of either a genetic change or a development change or, most probably, both – was a common cognitive feature in at least *H. sapiens* prior to the expansion from Africa. In other words, most – if not all – members of this reduced group shared the same cognitive (linguistic) endowment. In the next sections we shall comment on whether we can say much the same concerning Neanderthals, which would allow us to talk about a much earlier scenario for recursion (before those hominid species split). Next, we review the theory that could accommodate a sudden autapomorphic (an apomorphy exclusive to a species) rising of recursion in *H. sapiens*.

3.2. On Gould and Lewontin's spandrel theory

Gould and Lewontin (1979) opposed an adaptationist understanding of the theory of evolution, by pointing out that it can give rise to mistakes by attributing functionality to features that may just be the outcome of structural constraints. In this regard, they recall Darwin's words about the possible number of factors that influence evolution[13] beyond natural selection, showing that Darwin himself did not believe that natural selection alone could explain any biological trait. The main critiques of the radical version of the *adaptationist* program are devoted to the core points that – in Gould and Lewontin's view – this program typically follows:

    1. An organism is atomized into "traits" and these are explained as structures optimally designed by natural selection; contrary to that,

---

[13]   "But as my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position -- namely, at the close of the Introduction -- the following words: „I am convinced that natural selection has been the main but not the exclusive means of modification." "This has been of no avail."
"Great is the power of steady misrepresentation; but the history of science shows that fortunately this power does not long endure." Darwin, (1870) final chapter of the sixth edition of *On the Origin of Species*.

Gould and Lewontin believe that organisms are integrated entities, not collections of discrete objects.

2. An organism cannot optimize each part without imposing expenses on others – here, Gould and Lewontin introduce the notion of "trade-off:" if an organism improves an element, another one becomes worse than before, following a kind of "compensation" rule.

3. Adaptationism usually assumes that if one adaptive argument fails, another must exist; its absence is due to the fact of an imperfect understanding of where an organism lives and what it does. This program also emphasizes immediate utility and excludes other attributes of form.

Against this program, Gould and Lewontin propose the concept of spandrel, a term borrowed from architecture, which defines the particular space that always arises between two arcs. They observe that this space, more or less triangular, is a necessary by-product of vaults. There is no possibility of avoiding it if one implements two arches. Hence, it would be wrong if, following adaptationism, one was to take for granted that spandrels are there for some function: some feats cannot be explained functionally but structurally. As a consequence, the authors apply this notion to biological evolution and consider the possibility that changes sometimes obey structural necessities and that the use these new changes will have is a secondary effect, arising from architectural, developmental or historical patterns. Finally they assert that "the immediate utility of an organic structure often says nothing at all about the reason for its being".

Both Bickerton (1996) and Gould (1997) have alluded to the concept of spandrel as a possible explanation for language emergence in humanity. Johansson (2005) correctly points out that Chomsky has also said something about it but without any clear reference to the "spandrel theory," and quotes Chomsky (1988), who, in Johansson's view, speaks in an "openly skeptical" manner about "the power of Darwinian evolution to bridge the gap[14]". In this regard, there is a clearer precedent in an interview in the early 80's by Huysbregts and Riemsdijk (Chomsky 1983). Concerning the spandrel option, Fitch (2005: 216–217) puts forward the following reflections:

---

[14]   On the contrary, what we see is skepticism about a gradualist evolutionary explanation for the emergence of language and based on Natural Selection only: "Evolutionary theory is informative of many things, but it has little to say, as of now, of questions of this nature [such as the origin of language].… In the case of such systems as language or wings it is not easy even to imagine a course of selection that might have given rise to them" (Chomsky 1988: 167). (quoted in Johansson 2005: 161).

> From the perspective advocated here, fractionating language into multiple interacting components, it is clear that the mechanisms compromising the FLB as a whole cannot be a spandrel. […] For something as recently evolved as language, and given the abstractness of many characteristics of language that interest linguists (such as recursion or subjacency), it would be surprising indeed if none of them were spandrels, in the sense of remaining unchanged from an initial exapted state. […] To demonstrate empirically that linguistic recursion is not a spandrel, we would need to show that it both functionally entails, and mechanistically exhibits, characteristics not found in social mindreading recursion.

Such an empirical proof has not been found yet; therefore, it is still reasonable to consider the possible spandrel nature of recursion. It would then be the result of mutation(s) and/or developmental changes – in this respect, we maintain an agnostic point of view; the quotation at the beginning of this work touches on this issue, but we shall not analyze what Chomsky understood as a "minor mutation," when writing the last lines of the epilogue of his manuscript.

 The spandrel view on the emergence of the neurocognitive apparatus that allows for the potentially massive production of structured mental patterns leads to the following question: if a spandrel is the by-product of a very specific combination of elements that always yields a final structure, what are the neurological and/or genetic building elements that provoke the recursion side-effect? What were the metaphorical arches that provoked the unexpected emergence of recursion?

On the other hand, the data offered by genetics on the temporal points of separation between *H. sapiens* and Neanderthals stress the fact that great qualitative differences in cognition would have been introduced in a seemingly short span of time – in fact, too short to make a genetic mutation the only factor responsible for the emergence of recursion. Regarding this, FHC (2005: 206) make the following statements more in tune with the Evo-Devo program:

> If it turned out that the capacity for recursion resulted from a phase transition in the pattern of neural connectivity that results automatically from increases in neocortex to subcortical tissue ratio, interacting with standard mammalian brain development, this would certainly be an interesting result.

4. Recursion before the split between *H. neanderthalensis* and *H. sapiens*?

How, then, does the spandrel hypothesis fit the available data from anthropological genetics? What can genetics tell us about the probable points of separation, speciation or emergence of *derived traits*[15] in *H. sapiens*? In Clark (2008) we find a genetic tree with different dates suggesting that just 200.000 years would have been enough for speciation (Figure 3).
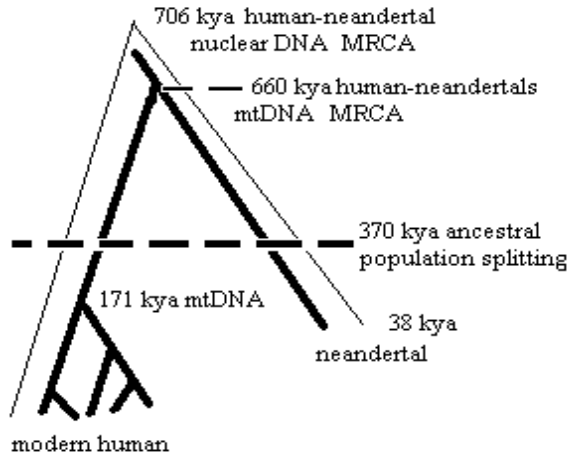

Figure 3. Genetic tree representing the dates the Most Recent Common Ancestors (MRCA) and speciation of Neanderthals and modern humans. Based on Clark (2008)

Although the last common nuclear DNA ancestor of both Neanderthals and sapiens can be found 706.000 years ago, the separation event of both populations (and hence the speciation process) occurred 370.000 years ago. The mtDNA common ancestor for modern humans is dated 171.000 years ago. In the meantime, that is ~200 kys (370 kys minus 171 kys), several different changes took place in both genomes[16] and/or developmental processes. One of the results was that *H. sapiens* developed a cognitive

---

[15]   In phylogenetics, a trait is derived if it is present in an organism but was absent in the last common ancestor of the group being considered. This may also refer to structures that are not present in an organism but were present in its ancestors, i.e. traits that have undergone secondary loss. Here the lack of a structure is a derived trait: e.g. the lack of laryngeal air sacs in *H. sapiens*. Hence, recursion might be such a trait.

[16]   Not much, since both species share 99.5% of the genome.

mechanism that allowed it to cognize embedded structures, which are arguably applied in music, language or maths. Did Neanderthal's divergent and isolated evolutionary path lead in the same direction?

The relatively brief span of time between the split event and the mtDNA common ancestor gives us ~200 kys, during which archaic *H. sapiens* would have developed the cognitive faculty of language until they reached the current form of human language. For that matter, the spandrel theory within an Evo-Devo conception could be applied to recursion, conciliating the brief span of time with the apparently abrupt and unexpected emergence of this biological innovation in modern humans proposed in HCF and FHC; a new change that would have rewired an important part of cognition, making possible not only the use of a powerful communication system, but also – if finally confirmed – other skills that might have been improved thanks to recursion, such as complex mathematical calculi or knotting. But such a scenario still does not clarify the moment in which this cognitive trait appeared.

4.1. Genetic similarities between *H. neanderthalensis* and *H. sapiens*

It is perfectly possible to conceive Neanderthal individuals sharing recursion with their sapiens cousins, as it is reflected in cladogram (a) in Figure 4.
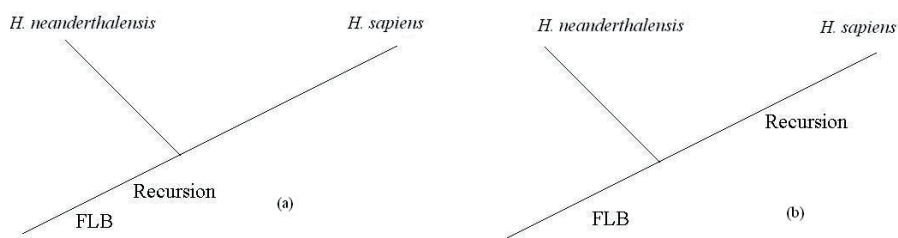

Figure 4. Cladograms representing two possibilities for the emergence of recursion: before and after Neanderthals and sapiens split off

The first Neanderthal genetic data come from short sequences of mtDNA obtained from the humerus of the type specimen by Krings *et al.* (1997). The first conclusions about such ancient DNA were that those sequences fell outside the range of variation of a diverse sample of modern humans. Interestingly, Neanderthals might have had a similar rate of genetic diversity to that of sapiens – mentioned in section 3.1 – that is, small, as Krings's *et al.*

(2000) experiments point out. And these are not the last coincident points between these two hominid species: experiments have shown that both species shared the same amino-acid sequence of the FOXP2 gene (Krause *et al*., 2007), a similar blood-group O (Lalueza-Fox *et al*., 2008) – though both were different to that of chimpanzees (Kermarrec *et al*., 1999). They even had a similar (though independently evolved) melanocortin receptor, which regulates pigmentation in humans and vertebrates or, in other words, some Neanderthals were also red-haired (Lalueza-Fox *et al*., 2007). Thus far, the coincident features between modern *H. sapiens* and *H. neanderthalensis* are several and could even be more than previously thought. Importantly, recent results from mtDNA seem to have solved a debate about several hominid remains found in Uzbekistan and in the Altai region of Siberia. Morphological analyses were not conclusive and both interpretations – either sapiens or Neanderthal – were proposed. Krause *et al*. (2007) have shown that those remains belong to a *H. neanderthalensis* of 37,750-years-old and 43,700-years-old respectively. These results imply that the traditionally accepted Neanderthal border has to be extended 2,000 km to the east, making the theory of a colonization of (part of) Asia by *H. neanderthalensis* more feasible. However, it is important to keep in mind the fact that until now, no genetic contribution has been found from the Neanderthal genetic pool to the modern human genetic pool, (Caramelli *et al*. 2003, Krings *et al*. 2000, 1997, Lalueza-Fox *et al*. 2006, Serre *et al*. 2004), though it is still possible that it will be found as Pääbo has repeatedly stated[17]. Therefore, arguments in favor of coincident cognitive capabilities, such as recursive patterning, should retract themselves to a temporal point prior to the split between these two hominids.

     Summing up, the available genetic data suggest some relevant insights into the evolution of language: 1) an African origin for modern humans and hence for language can be argued; 2) these data do not imply nor

---

     [17]   In this respect it is worth bearing Clark's words (2008) – suggesting three possible scenarios – in mind:

1) If there had been admixture, say 100,000 years ago, giving, modern humans small segregating pieces of our genome with Neanderthal ancestry, it would be nearly impossible to identify them as such, even with full genome sequences.

2) […] Nordborg (1998) pointed out that mtDNA follows clonal haploid transmission, and so the genealogy inferred from mtDNA is only one sample among millions of possible genealogies. Admixture could have easily occurred without leaving any trace in current mtDNA sequences.

3) [...] Also, perhaps the interbreeding was strictly unidirectional; for example, only human female by Neanderthal male matings occurred and never the reverse. This would yield modern humans with admixed nuclear genes but a complete absence of Neanderthal mtDNA.

exclude an earlier emergence of recursion, due to strong genetic similarities between *H. neanderthalensis* and *H. sapiens*; 3) but, if recursion is a sapiens autapomorphy, there is need of an explanation that can account for such a sudden change (cf. section 3.2 for a possible one); 4) recursion does not need to be, *per se,* the (by)product of mutation only, since in combination with genetic change there could have been developmental changes, too.

However, it is still possible to explore samples of recursive behaviour in the Upper Paleolithic with a view to finding archaeological traces of recursion.

4.2. Recursion and archaeological record

If we still cannot target the genetic and/or developmental change in modern human DNA that favored the great leap in human cognition, maybe, we could find traces of that in the archaeological record. Regarding recursion, there is obvious difficulty in finding and showing its presence, since it does not fossilize. We recall here FHC's words about the range of action of recursion:

> Accepting for a moment our provisional, tentative assignment of FLN of only recursion and mapping to the interfaces, it seems clear that the current utility of recursive mental operations is not limited to communication. (FHC 2005: 186)

Hoffecker (2007) argues that it is possible to recognize recursive behaviour in Middle Paleolithic artifacts which correspond to the Levallois technique:

> At this site [Biache-Saint-Vaast, France], blade-like flakes of predetermined size and shape were produced by a hierarchically organized sequence of removals from a prepared core. … Variations in the direction and size of the flake removals reveal some recursive combinations within the embedded hierarchical levels." (Hoffecker 2007: 371; square brackets added, LBC)

However, as the author himself admits "prepared core technology has late Acheulean roots". Cela-Conde and Ayala (2007) comment that "The Levallois technique appeared during the Acheulean period, and was used thereafter. Its pinnacle was reached during the Mousterian culture." Thus, this material culture flourished in Europe and the Near East; therefore, there has repeatedly been a consistent identification between the Mousterian culture and *H. neanderthalensis*, despite the inherent difficulty in associating a given

species with a cultural tradition. In other words, Hoffecker's approach would imply that Neanderthals could have made some use of recursion. It is true that this general conception about the systematic Neanderthal-Mousterian link has been questioned after the excavations carried on in the Near East, where a later occupation by *H. neanderthalensis* was certified, at sites which had already been inhabited by anatomically modern humans (Bar-Yosef & Vandermeersch 1993).

According to Hoffecker, some tools, such as *scrapers*, would have been made following some kind of recursive process; in his proposal, he appropriately interprets an order of the flaking process that such tools underwent. Nevertheless, beyond the enumeration of some of the hits, no system or model has been offered that fully explains the manufacturing of the tools and that convinces us that the same kind of recursion is used in both language and tool making. Though we admit a coincident intuition regarding recursion and tool making – that is, it should, in fact, be possible to infer recursion in some non-linguistic behaviours – further research is required to assess that the same cognitive mechanism is acting in both modern human language and Mousterian tool manufacturing.

4.2.1. Recursive patterning in knotting and netting

An additional problem in this kind of approach has been hinted at by Camps and Uriagereka (2006) in their study on knotting. Taking into account an intuition left on a draft by Mount (1989) – according to which knots could be developed by some kind of Context-Sensitive grammar (*a fortiori*, by a recursive grammar) – Camps and Uriagereka try to answer the following questions: is this kind of grammar the only one able to process an activity such as knotting? What about other hominids? Is there available evidence of knotting beyond the Upper Paleolithic? The authors contend that Context-Sensitive (when recursive) and Finite-State (iterative) grammars do not yield the same results. The difference is that the latter needs more memory and steps to yield the same endpoint. In other words, recursion would be clearly beneficial for complex activities such as knotting. The second conclusion is that, while there is evidence of knotting in the Upper Paleolithic which can be attributed to anatomically modern humans, this is not true for Neanderthals. According to Camps and Uriagereka, there is still no clear evidence that the hafted Mousterian points were attached to wooden shafts by means of knots. Indeed, the authors argue that "Mousterian projectile technology implies hafting, but not obviously the ability to make knots; in contrast, when it

comes to the M[iddle] S[tone] A[ge] projectile technology, use of knots can arguably be inferred"(Camps & Uriagereka 2006: 52).

Interestingly, d'Errico (2003) shows that the *hafting* technique is not an innovation of modern humans, given that at several Mousterian sites from Levant[18] there have been found traces of *bitumen*, a kind of glue material used for hafting. D'Errico points out that in the Near East there is clear evidence of hafting, blades and burials which can be attributed to both species (cf. d'Errico 2003: 200, Figure 8). The Near East seems to be a place where both species might have been in touch with each other and even might have coexisted in some areas. Whether there was a transfer of cultural traditions is still contentious[19]. Moreover, an associated activity, netting, is only found in anatomically modern humans sites (Adovasio *et al*. 1997, Adovasio *et al*. 2005).

Species do not always exploit all their potential and capabilities simply because it is not always required by the environment. Experiments carried out with apes and monkeys have shown that the capabilities of these primates are greater than those exhibited in natural conditions,[20] although it is true that several of the possible behaviours have only been found in the laboratory. However, even if Neanderthals could have been capable of knotting, it is also true that this is a complex process that has been exploited in some cultures more than in others. On the one hand, some cultures placed in the vicinity of great volumes of water have developed a very intriguing and complex collection of knots, very useful for fishers. On the other hand, other cultures, such as those of the Aborigines in Australia, make use of the *atl-atl* and the *boomerang* instead of a bow – the introduction of flake-based assemblages seems to be quite recent (d'Errico 2003) – although they, like all *H. sapiens*, are absolutely capable of making knots.

Finally, we are obliged to reference the most impressive pieces of archaeological record found until now concerning recursive patterns: the

---

[18]   Paleoanthropologists call "Levant" the area of the current Near East; then it was the "Levant" ("east") of the "Neanderthals' land."

[19]   Cf. d'Errico *et al.* (1998) for an interesting debate about whether or not there was Neanderthal acculturation in Western Europe caused by the arrival of modern humans.

[20]   For example, experiments seem to support the idea that baboons could recognize hierarchical classifications by rank and kinship (Bergman *et al*. 2003), that chimpanzees are rational maximizers in an Ultimatum Game (Jensen, *et al*. 2007), can perceive causality (O'Connell & Dunbar 2005) and understand some psychological states (Tomasello *et al*. 2003), that bonobos and orangutans save tools for future use (Mulcahy & Call 2006), or that the endowment effect has been detected in Capuchin monkeys (Lakshminaryanan, *et al*. 2008). But see Penn *et al*. (2008) for a rather critical view of most assumptions made in this field.

stones and the perforated beads found in the Blombos cave in South Africa (Henshilwood *et al*. 2009, Henshilwood *et al*. 2002). Regarding the beads, there are obvious reasons to think that they were ornaments and that they were knotted somehow. Concerning the stones, they were engraved with a very interesting pattern of lines, resembling a succession of rhombus. On one of the stones (item SAM-AA 8938), this patterning is much clearer than on the other (item SAM-AA 8937), with the geometric figures "better designed" so to speak, which leads one to speculate whether the worst of the pair was a first trail. In any case, the intentionality of the "artist" seems to be out of the question. Camps and Uriagereka have already pointed out that such a geometric picture could theoretically be described by a Context-Sensitive Grammar, though they do not offer a more extensive account of such a grammar.

For these reasons, a scenario can be conceived in which, using cognitive computational terms, Neanderthals were potentially able to make knots but never developed such an ability until they got in touch with modern humans. Nevertheless, a second scenario we can figure out is related to the possible emptiness of FLN we mentioned in the first section: Neanderthals had recursion, but the divergent (both genetic and developmental) evolution of their brains provoked the emergence of different kinds of mappings. When the process of speciation became a reality (as current genetic data seem to suggest), two different kinds of cognition had arisen. This is in tune with the following statements HCF make after quoting the third definition (cf. the first section of this paper):

> To be precise, we suggest that a significant piece of the linguistic machinery entails recursive operations, and that these recursive operations must interface with SM and CI. … These mappings themselves could be complex (though we do not know) because of conditions imposed by interfaces. FHC (2005: 182) [emphasis added: LBC]

Finally, there is a third scenario supported by the strong hypothesis according to which Neanderthals could have lacked recursion as it is understood in linguistics, that is, as a core element for complex computations and linguistic structures. If recursion belongs first to language, as some people argue, and then has been reused in other cognitive domains, Neanderthals, lacking linguistic recursion, would have never been able to reuse it or co-opt it for making knots (as suggested by the, still negative, evidence), nor to speak exactly in the way that anatomically modern humans

do. This hypothesis will be falsified as soon as archaeological record linking *H. neanderthalensis* and recursive activity is established.

To conclude, we see that neither the current data from genetics, nor from paleoanthropological records, nor from comparative psychology allow us to exclude the hypothesis according to which Neanderthals might have had recursion. For this reason, it is not impossible to conceive of a Neanderthal hominid executing and processing recursive patterns, but the fact is that there is still no proof of that. Hence, we still cannot assess nor include recursion in the cladogram before the split point between these two hominid species – with the exception of the starlings case, as a homoplasy case, if finally confirmed.

5. Conclusions

As we have seen, the evolution of language cannot be addressed from the perspective of a single discipline; others, such as genetics or archaeology, also have a say on this issue. There is still a lot of research needed regarding Neanderthal cognition, an issue that deserves more attention also by biolinguistics. Although there are reasons to think so, the available data do not allow us to exclude recursion either from the cognition of *H. neanderthalensis* or starlings. Thus, what can be called *special* in humans or in language?

The last part of the next quotation may summarize almost perfectly our own hypothesis about the role of recursion in language and in the whole cerebral architecture related to linguistic and non-linguistic activity.

> *Something* about the faculty of language must be unique in order to explain the differences between humans and the other animals – if only the particular combination of mechanisms in FLB. (FCH 2005: 182).

The search for the single trait that makes modern humans special seems to lead us to the conclusion that it is the specific combination of the elements which enabled the emergence of human cognition, and maybe – as cognitive spandrels – of human-specific capacities such as recursive patterning, recursive language, perception of beauty and moral sense (Nadal, *et al*. 2009). Further interdisciplinary research is needed in order to achieve a satisfactory account not only of the origins of recursion, but also of its autapomorphic character in *H. sapiens* and its biological nature.

Acknowledgments

References

Adovasio, J.M., Hyland, D.C., & Soffer, O. (1997). Textiles and cordage: a preliminary assessment. In J Svoboda,. (Ed.), *Pavlov I – Northwest. The Upper Paleolithic Burial and Settlement Context.* (Vol. 4, pp. 432–443). Dolní Věstonice Studies.

Adovasio, J.M., Soffer, O. & Hyland, D.C. (2005). Textiles and cordage. In J Svoboda. (Ed.), *Pavlov I Southeast. A Window into the Gravettian Lifestyles* (Vol. 14, pp. 432–443). Dolní Věstonice Studies.

Bar-Yosef, O. & Vandermeersch, B. (1993). Modern humans in the Levant. *Scientific American*, *268*(4), 94–100.

Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical classification by rank and kinship in baboons. *Science (New York, N.Y.)*, *302*(5648), 1234–6.

Bickerton, D. (1996). *Language and Human Behavior*. University of Washington Press.

Boë, L., Heim, J., Honda, K. & Maeda, S. (2002). The potential Neandertal vowel space was as large as that of modern humans. *Journal of Phonetics*, *30*(3), 465–484.

de Boer, B. (2007). Investigating the acoustic effect of the descended larynx with articulatory models. *ACLC working papers*, *2*, 61–86.

Camps, M., & Uriagereka, J. (2006). The Gordian Knot of linguistic fossils. In J. Rosselló, Joana & Martín, Jesús (Eds.), *The Biolinguistic Turn. Issues on Language and Biology* (p. 278). Barcelona: PPU, S.A.

Cann, R. L., Stoneking, M., & Wilson, A. C. (1983). Mitochondrial DNA and human evolution. *Nature*, *325*(6099), 31–6.

Capelli, C., Wilson, J. F., Richards, M., Stumpf, M. P., Gratrix, F., Oppenheimer, S., Underhill, P., *et al.* (2001). A predominantly indigenous paternal heritage for the Austronesian-speaking peoples of insular Southeast Asia and Oceania. *American Journal of Human Genetics*, *68*(2), 432–443.

Caramelli, D., Lalueza-Fox, C., Vernesi, C., Lari, M., Casoli, A., Mallegni, F., Chiarelli, B., *et al.* (2003). Evidence for a genetic discontinuity between Neandertals and 24,000-year-old anatomically modern Europeans. *Proceedings*

of the National Academy of Sciences of the United States of America, *100* (11), 6593–7.

Cela-Conde, C. J., & Ayala, F. J. (2007). *Human Evolution: Trails from the Past* (1red.). Oxford University Press, USA.

Clark, A. G. (2008). Genome sequences from extinct relatives. *Cell*, *134*(3), 388–389.

Coleman, J., Kochanski, G., Rosner, B., & Grabe, E. (2004). Letter on "Computational Constraints on Syntactic Processing in a Nonhuman Primate". *Science*, *303*, 377–380.

Chiaroni, J., Underhill, P. A., & Cavalli-Sforza, L. L. (2009). Y chromosome diversity, human expansion, drift, and cultural evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(48), 20174–20179.

Chomsky, N. (2008). The biolinguistic program: where does it stand today? Unpublished, MIT.

Chomsky, N. (1983). *Noam Chomsky on the Generative Enterprise: A Discussion*. Foris Pubns USA.

Chomsky, N. (2010). Some simple evo devo theses: how true might be for language? In R. K. Larson, V. Déprez, & H. Yamakido (Eds.), *The Evolution of Human Language: Biolinguistic Perspectives* (1r ed.). Cambridge University Press.

D'Errico, F. (2003). The invisible frontier. A multiple species model for the origin of behavioral modernity. *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(4), 188–202.

d'Errico, F., Zilhão, J., Julien, M., Baffier, D., & Pelegrin, J. (1998). Neanderthal Acculturation in Western Europe? A Critical Review of the Evidence and Its Interpretation. *Current Anthropology*, *39*(s1), S1–S44.

Endress, A., Cahill, D., Block, S., Watumull, J., & Hauser, M. (2009). Evidence of an evolutionary precursor to human language affixation in a non-human primate. *Biology Letters*.

Everett, D. L. (2005). Cultural Constraints on Grammar and Cognition in Pirahã Another Look at the Design Features of Human Language. *Current Anthropology*, *46*(4), 621–646.

Fitch, W. T., & Reby, D. (2001). The descended larynx is not uniquely human. *Proceedings. Biological Sciences / The Royal Society*, *268*(1477), 1669–75.

Fitch, W. T., & Hauser, M. D. (2004). Computational constraints on syntactic processing in a nonhuman primate. *Science (New York, N.Y.)*, *303*(5656), 377–80.

Fitch, W. T., Hauser, M. D., & Chomsky, N. (2005). The evolution of the language faculty: clarifications and implications. *Cognition*, *97*(2), 179–210; discussion 211–225.

Fitch, W. T. (2002). Comparative Vocal Production and the Evolution of Speech: Reinterpreting the Descent of the Larynx. In Alison Wray (Ed.), *The Transition to Language*. Oxford: Oxford University Press.

Fitch, W. T. (2005). The Evolution of Language: A Comparative Review. *Biology & Philosophy*, *20*(2–3), 193–203.

Fitch, W. T. (2010). Three meanings of "recursion": key distinctions for biolinguistics. In R. K. Larson, V. Déprez, & H. Yamakido (Eds.), *The Evolution of Human Language: Biolinguistic Perspectives* (1r ed.). Cambridge University Press.

Fujita, Koji. (2009). A Prospect for Evolutionary Adequacy: Merge and the Evolution and Development of Human Language, *3*(2–3), 128–1253.

Gentner, T. Q., Fenn, K. M., Margoliash, D., & Nusbaum, H. C. (2006). Recursive syntactic pattern learning by songbirds. *Nature*, *440*(7088), 1204–1207.

Gould, S. J. (1997). The exaptive excellence of spandrels as a term and prototype. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(20), 10750–10755.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B, Containing Papers of a Biological Character. Royal Society (Great Britain)*, *205*(1161), 581–598.

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: what is it, who has it, and how did it evolve? *Science (New York, N.Y.)*, *298*(5598), 1569–79.

van Heijningen, C. A. A., de Visser, J., Zuidema, W., & ten Cate, C. (2009). Simple rules can explain discrimination of putative recursive syntactic structures by a songbird species. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(48), 20538–20543.

Henshilwood, C. S., d'Errico, F., & Watts, I. (2009). Engraved ochres from the Middle Stone Age levels at Blombos Cave, South Africa. *Journal of Human Evolution*, *57*(1), 27–47.

Henshilwood, C. S., d'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G. A. T., Mercier, N., *et al.* (2002). Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science (New York, N.Y.)*, *295*(5558), 1278–1280.

Hockett, Charles F. (1958). *Course in Modern Linguistics* (later Printing.). Prentice Hall College Div.

Hockett, Charles F. (1960). The origin of speech. *Scientific American*, *203*, 89–96.

Hoffecker, J. (2007). Representation and Recursion in the Archaeological Record. *Journal of Archaeological Method and Theory*, *14*(4), 359-387.

Honda, Kiyoshi, & Tiede, Mark K. (1998). An MRI study on the relationship between oral cavity shape and larynx position. *ICSLP-1998*, (0686).

Jackendoff, R., & Pinker, S. (2005). The nature of the language faculty and its implications for evolution of language – (Reply to Fitch, Hauser, and Chomsky). *Cognition*, *97*(2), 211–225.

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science (New York, N.Y.)*, *318*(5847), 107–109.

Johansson, S. (2005). *Origins Of Language: Constraints And Hypotheses (Converging Evidence in Language and Communication Research*. John Benjamins Publishing Co.

Kaessmann, H., Wiebe, V., Weiss, G., & Pääbo, S. (2001). Great ape DNA sequences reveal a reduced diversity and an expansion in humans. *Nature Genetics*, *27*(2), 155–6.

Kermarrec, N., Roubinet, F., Apoil, P. A., & Blancher, A. (1999). Comparison of allele O sequences of the human and non-human primate ABO system. *Immunogenetics*, *49*(6), 517–26.

Kochanski, G. (n.d.). Comment on Fitch and Hauser, "Computational Constraints...". Retrieved January 8, 2010, from http://kochanski.org/gpk/papers/2004/FitchHauser/

Krause, J., Lalueza-Fox, C., *et al.* (2007). The derived FOXP2 variant of modern humans was shared with Neandertals. *Current Biology: CB*, *17*(21), 1908–12.

Krause, J., Orlando, L., *et al.* (2007). Neanderthals in central Asia and Siberia. *Nature*, *449*(7164), 902–904.

Krings, M., Capelli, C., Tschentscher, F., Geisert, H., Meyer, S., von Haeseler, A., Grossschmidt, K., *et al.* (2000). A view of Neandertal genetic diversity. *Nature Genetics*, *26*(2), 144–6.

Krings, M., Stone, A., Schmitz, R. W., Krainitzki, H., Stoneking, M., & Pääbo, S. (1997). Neandertal DNA sequences and the origin of modern humans. *Cell*, *90*(1), 19–30.

Kuhl, P. K., & Miller, J. D. (1975). Speech perception by the chinchilla: voiced-voiceless distinction in alveolar plosive consonants. *Science (New York, N.Y.)*, *190*(4209), 69–72.

Lakshminaryanan, V., Chen, M. K., & Santos, L. R. (2008). Endowment effect in capuchin monkeys. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1511), 3837–3844.

Lalueza-Fox, C., Gigli, E., de la Rasilla, M., Fortea, J., Rosas, A., Bertranpetit, J., & Krause, J. (2008). Genetic characterization of the ABO blood group in Neandertals. *BMC Evolutionary Biology*, *8*, 342.

Lalueza-Fox, C., Krause, J., Caramelli, D., Catalano, G., Milani, L., Sampietro, M. L., Calafell, F., *et al.* (2006). Mitochondrial DNA of an Iberian Neandertal suggests a population affinity with other European Neandertals. *Current Biology: CB*, *16*(16), R629–30.

Lalueza-Fox, C., Römpler, H., Caramelli, D., Stäubert, C., Catalano, G., Hughes, D., Rohland, N., *et al.* (2007). A melanocortin 1 receptor allele suggests varying pigmentation among Neanderthals. *Science (New York, N.Y.)*, *318*(5855), 1453–5.

Liberman, Mark. (2004, January 17). Language Log: Hi Lo Hi Lo, it's off to formal language theory we go. *Language Log*. Retrieved January 8, 2010, from http://itre.cis.upenn.edu/~myl/languagelog/archives/000355.html

Lieberman, P. (1973). On the evolution of language: a unified view. *Cognition*, *2*, 59–94.

Lieberman, P., & Crelin, E. S. (1971). On the speech of neandertal man. *Linguistic Inquiry*, *2*, 203–222.

Lieberman, P., Klatt, D. H., & Wilson, W. H. (1969). Vocal tract limitations on the vowel repertoires of rhesus monkey and other nonhuman primates. *Science (New York, N.Y.)*, *164*(884), 1185–7.

Mount, John. (1989). KnotEd: a program for studying knot-theory. Hewlett-Packard, Cupertino. Retrieved from http://mzlabs.com/JohnMount/index.html

Mulcahy, N. J., & Call, J. (2006). Apes save tools for future use. *Science (New York, N.Y.)*, *312*(5776), 1038–1040.

Nadal, M., Barceló-Coblijn, L., Olivera, A., Christensen, J. F., Rincón-Ruíz, C., & Cela-Conde, C. (2009). Darwin's Legacy: A comparative approach to the evolution of human derived cognitive traits. *Ludus Vitalis*, *32*.

Nazzi T., Jusczyk P.W., & Johnson E.K. (2000). Language Discrimination by English-Learning 5-Month-Olds: Effects of Rhythm and Familiarity. *Journal of Memory and Language*, *43*, 1–19.

O'Connell, S., & Dunbar, R. I. M. (2005). The perception of causality in chimpanzees (Pan spp.). *Animal Cognition*, *8*(1), 60–66.

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys use affixation to alter call meaning. *PloS One*, *4*(11), e7808.

Parker, A. R. (2006). Evolving the narrow language faculty: was recursion the pivotal step? *Proceedings of the 6th International Conference on the Evolution of Language*, 239–246.

Penn, D. C., Holyoak, K. J., & Povinelli, D. J. (2008). Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *The Behavioral and Brain Sciences*, *31*(2), 109–130; discussion 130–178.

Perruchet, P., & Rey, A. (2005). Does the mastery of center-embedded linguistic structures distinguish humans from nonhuman primates? *Psychonomic Bulletin & Review*, *12*(2), 307–13.

Pinker, S., & Jackendoff, R. (2005). The faculty of language: what's special about it? *Cognition*, *95*(2), 201–236.

Ramus, F., Hauser, M. D., Miller, C., Morris, D., & Mehler, J. (2000). Language discrimination by human newborns and by cotton-top tamarin monkeys. *Science (New York, N.Y.)*, *288*(5464), 349–51.

Recursive Functions (Stanford Encyclopedia of Philosophy). (n.d.). Retrieved February 8, 2010, from http://plato.stanford.edu/entries/recursive-functions/

Serre, D., Langaney, A., Chech, M., Teschler-Nicola, M., Paunović, M., Mennecier, P., Hofreiter, M., *et al.* (2004). No evidence of Neandertal mtDNA contribution to early modern humans. *PLoS Biology*, *2*(3), E57.

Stebbins, J. R. (2007). The Evolution of Evolutionary Linguistics. *Colorado Research in Linguistics*, *20*(1).

Stumpf, M. P., & Goldstein, D. B. (2001). Genealogical and evolutionary inference with the human Y chromosome. *Science (New York, N.Y.)*, *291*(5509), 1738–1742.

Tincoff, R., Hauser, M., Tsao, F., Spaepen, G., Ramus, F., & Mehler, J. (2005). The role of speech rhythm in language discrimination: further tests with a non-human primate. *Developmental Science*, *8*(1), 26–35.

Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees understand psychological states – the question is which ones and to what extent. *Trends in Cognitive Sciences*, *7*(4), 153–156.

Toro, J. M., Trobalon, J. B., & Sebastián-Gallés, N. (2003). The use of prosodic cues in language discrimination tasks by rats. *Animal Cognition*, *6*(2), 131–6.

de Vries, M. H., Monaghan, P., Knecht, S., & Zwitserlood, P. (2008). Syntactic structure and artificial grammar learning: the learnability of embedded hierarchical structures. *Cognition*, *107*(2), 763–774.