A Biolinguistic Aproach to the Mosaic of

H. neanderthalensis Vocalizations

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In the present work I revisit the old question about the possibilities and aptitudes the *H. neanderthalensis* had for vocalization. I discuss new evidence that moves the discussion beyond traditional interest in the presence and interpretation of the fossil record and its comparison with the closest species to *H. sapiens*, like chimpanzees and gorillas. I apply to the analysis an interdisciplinary perspective and gather information from neuropsychology, genetics and comparative psychology. This procedure is useful to conform the aimed vision in biolinguistics, so that the neurocognitive activity becomes important thanks, above all, to the comparison with other species. Finally, I conclude that the hypothesis about the formation of a vocal capacity previous and independent to the cognitive faculty of language is plausible, and that Neandertals were probably able of vocalizing voluntarily, with communicative intentions and in a sophisticated way.

Keywords: H. neanderthalensis; hyoid bone; von Economo neurons; vocal tract; air sacs

1. Introduction

The issue about language and the communicative possibilities is not new at all and indeed, it has been revisited from time to time. Intuition has traditionally told us that, at the moment when both hominins -H. sapiens and H. neanderthalensis - met, they had to be able to establish some kind of communicative interaction. This kind of thought has led people to take for granted that Neandertals possessed a cognitive faculty of language like modern humans do. I argue that - though possible -, contrary to that first impression and to what could apparently be the most obvious ("what the common sense tells us"), it is not so obvious that H. neanderthalensis could communicate as we do. Moreover, I will put forward the idea that vocalization is a capacity almost nearly independent from the capacity

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we humans have of creating linguistic constructions which can be conflated to semantic macro-concepts - though it could have co-evolved along with this latter capacity. Thus far, our approach takes pieces of evidence from several areas of science in an attempt of contributing with a much wider vision than that we can get from the hyoid bone only. Thus, von Economo neurons can be good targets for research in vocalization: we know that within primates, only great apes have these kind of neurons (orangutans, gorillas, chimpanzees, bonobos and humans). Such neurons are located, specially, in the anterior cingular cortex, an area related to, among other functions, vocalization. Other data about vocalization are taken from genetics, for example, the well-known FOXP2, which has been showed to be present in both Neandertals and modern humans. In this sense, I will apply a quite classic methodology in the most traditional philology: when one has not got the written proof of a lexical form that could have existed, but there is certainty of it due to other indirect evidences – for example, linguistic comparison, or linguistic reconstruction –, a symbol (*) is applied to the alleged word, while waiting to find a document that can prove it. Instead, if one thinks that there are not proofs enough, or that they are not conclusive, a symbol (X) will be applied. In the case of a positive conclusion, the symbol will be $(\sqrt{})$. Let's see some samples not directly related with vocalization:

Trait	H. neanderthalensis	H. sapiens	
Bipedalism			
Chin	X	$\sqrt{}$	
Hiperboreal adaptation	*	X	

Table 1

So, we can see how "bipedalism" is clearly inferible from the osseous morphology and hence both species have a confirmation symbol for this trait. Instead, "chin" is confirmed in *H. sapiens*, but discarded in the *H. neanderthalensis* case. Finally, "hiperboreal adaptation" is clearly absent in modern humans, but not fully rejectable in the case of Neandertals. For this reason, because it is not sure, but there are signs pointing that this could be a trait of this species, I apply an asterisk, indicating that this is a viable option, although more proofs and research are needed in order to finally confirm it.

Next, I will review some traits I consider particularly relevant regarding human vocalization, and I will try to extrapolate them to the Neadertal case, in order to draw some conclusions that help me offer a more complete picture of the issue. Traditionally (and understandably), attention has specially been focused on the analysis of fossil record, that could reliably indicate a linguistic capacity in this species, evolutionary so close to *H. sapiens*. As we will see, the issue has become more complicated than previously thought. Even some apparently insurmountable obstacles like the fact that brain does not fossilize, can be overcome in a minimal (but substantial) way, thanks to the interdisciplinary work. Data from different scientific fields come together, in such a way that different

areas become linked and the issue can be studied from different, but confluent perspectives. One of the methods I will make use of, is the comparative method. Comparison between species provides us with clues about what is inferible from other species through homologies and convergences. However, I am aware of the limitations of this method and of the necessary caution in order to deal with the presence or absence of a particular trait in a extinct species.

Next, I show a succinct list of the traits that will be object of analysis in the present work:

Trait	Brief Definition
Larynx	It is an organ for phonation, an air conduct and a sphinteric mechanism which goes from the base of the tongue to the traquea.
Vocal Tract	Animal cavity where the sound that is produced in its source (the larynx) is filtered.
von Economo Neurons	Neurons characterized by its spindle shape only present in the anterior cingular cortex, disgranular prefrontal cortex and in the frontal insula.
Lack of air sacs	Absence of laryngeal air sacs which were connected to the hyoid bone.
Mirror Neurons	Neurons that fire when the animal performs or observes an action by a conespecific.
FOXP2	Gene and protein related to specific language impairments.
Region 2-4 kHz	Region of the sound wave curve that contains relevant acoustic information for humans.

Table 2

As we can see, the traits in table 2 go above the traditional way the problem of vocalizations in extinct hominids has been set out. So, I have bet for interdisciplinary work, and import information from genetics, neuropsychology and from acoustic models. This implies that the vocal apparatus loses (part of) the leading role, in favor of an approach that integrates some brain regions and more concretely the role of some neurons that in the last years have been considered capital regarding those aspects of human cognition related with language and communication, respectively. Thus, for vocalization, it is not just anatomy what matters, but also the neural areas involved in its control.

This work is structured as follows: in the first part I will review the literature dealing with larynx reconstructions and the great (still enduring) debate arisen around this cavity of the vocal apparatus. This implies both the discussions about the lowering of larynx as a trait characteristic of modern human beings, and the discussions about the role of the hyoid bone in the larynx; and also the possible autapomorphic character of the morphology of this bone in modern

humans regarding the rest of great apes. I will discuss the hyoid bone in connection with its lack of the orifice where the so-called air sacs are connected, which are present in all great apes but humans.

In order to avoid ambiguities, I will use some traditional concepts from cladistics which are very useful to describe characters of particular species, particularly specific changes that attract the attention of scientifs. Thus, in cladistics (see Kitching *et al.* 1998), a derived change is called *apomorphy*. Whereas adding to it the prefix *sin-*, it indicates that the character is shared with other species and their common ancestor, the prefix *auta-* indicates that the character is an exclusive novelty of a particular species. Instead, a *homoplasy* is a new character shared by two or more non-related species.

- An example of an autapomorphy is the loss of hair in humans, regarding the rest of primates.
- An example of a sinapomorphy is the loss of hair in cetaceans regarding the rest of mammals.
- An example of a homoplasy are the wings in bats and birds.

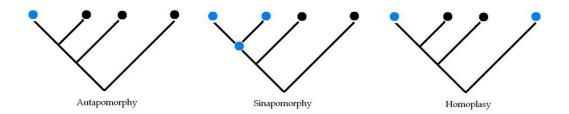


Figure 1: Cladistic concepts

The second part, as if it were an extension of the previous one, is devoted to the perceptive capacity of modern humans which, as it seems, could have coevolved along with the rest of the vocal apparatus. An evolutionary perspective suggests that, in order to produce distinctive vocal sounds, we have first to be able of perceiving them adequately because such feedback is required to imitate them. Thus, I will explore the cognitive abilities related to both production and perception and we will see how they – according to experimental work in this field on the one hand, and to the comparative method on the other hand – could have been very similar in the hominid ancestors of *H. sapiens*, like the *H. heidelbergensis*, and, by extension, the *H. neanderthalensis*.

In the third section I change the topic and I go on dealing with an aspect I consider capital regarding all what surrounds language: the neuronal apparatus that sustains human cognition. I take an integrative view, according to which the brain has neither evolved *de novo*, nor layer after layer, as if the only new and mutable part were just the cortex. The approach I put forward agrees with a vision of the brain, according to which this organ has undergone different selective pressures and hazardous episodes (e.g. mutations) that made possible, not only the expansion of old areas (e.g. prefrontal cortex), but also the slow and gradual modification of already extant structures (e.g. current basal ganglia). It is because of this, that I take cautious measures when inferring the presence of certain neurons that have attract attention in the last years: on the one hand, the mirror

neurons, and on the other hand the *von Economo* neurons. The former have been detected in several representatives of the primate world and it is argued that they could also be part of human brains; the latter is a kind of neurons evolutionary very new in primates and, in fact, they are present in only one family of hominoids: the *Hominidae* (see fig. 2), which covers the current five species of great apes; these neurons are particularly numerous in the tribe *Hominini* (both genera *Homo* and *Pan*).

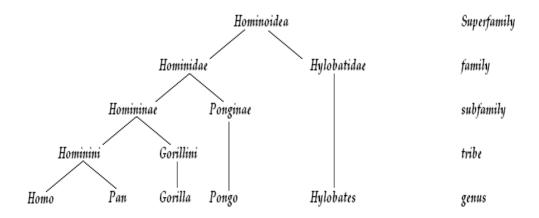


Figure 2: Classification of Hominoidea

The classification of hominids is a burning issue in the current debate of the evolution of human beings. Their ancestors are many and the possibilities that one of them was our direct precursor are several. The classification I show next is just one of the among the possible ones, and pretends to be a reference frame, rather than a firm proposal. However, I have included a mark in reference to a variant proposed by Wood & Collard (1999), according to which the current genus *Homo* would have begun with the *H. erectus*. I take into account this approach about the genus *Homo* because it reorganizes the vision one could have about a particular fact related to speech.

I will also talk about some molecular aspects that can affect neurons. Thus, this section is also devoted to a scientific field that day by day provides us of new and determinant information about organic structure, its ontogeny and its phylogeny, that is to say, genetics. So, I will review succinctly the most important aspects of the gen *FOXP2* (and of its protein) as regards vocalization and the role it plays in the control of orofacial muscles, and other genes related to sound perception as well. The former gene is interesting because is related to some language impairments, but also because the dating of its evolution is quite recent and it could be circumscribed to the genus *Homo* or even only to a subset of it.

Finally, yet at the conclusions, I defend the idea that the question of the

vocalization is to some good extent independent of the emergence – in *H. sapiens* – of a capacity until now without detected counterparts in any other species, which make us able of creating meaningful linguistic structures, and coding thoughts and reflections, the number of which seems to be endless. Moreover, due to the analysis I have made in the previous sections, I will also defend the idea that the critic point of Neandertal vocalization – once separated from the above mentioned capacity – is whether or not this hominin had the same capabilities for motor control of orofacial and lingual muscular structures, and as a last resort, the same cognitive capabilities (i.e. the phonetic and phonological aspects).

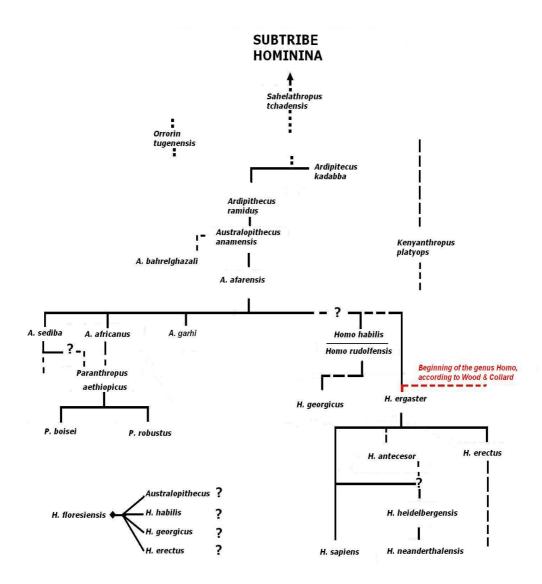


Figure 3: A possible classification of the subtribe Hominina

2. On vocal apparatus reconstructions. The archaeological method.

The issues about the linguistic capacity in other species different from H. sapiens have been a topic for debate since long time. Nevertheless, the lack of data forced sometimes the researchers to get into a high level of speculation; so much so that in 1866 the Société de Linguistique from Paris banned this topic as suitable for scientific research. The discovering of Neadertal remains and its acknowledge as a species, turned out the status of the modern human and now this "cousin" is seen somehow as a kind of "rival". The modern human had been considered by many of people as the final milestone of evolution. Since then, there has appeared a necessity for looking for the factor that makes us humans. One of such proposals was language. This apparently only human capacity became center-stage in a great debate that endures still nowadays. Language attracted attention in the evolutionary debate, due to its potential explanations of facts still on discussion, like the extinction of Neandertals¹. Leaving aside the suddenly enormous responsibility that speech acquired regarding the possibilities for survival of a species, Lieberman says, however, one thing is true, that posterior studies have confirmed – although it is by and large not so radical in their conclusions: a language or any other social factor like religion could be, in some cases, an important factor, if not essential, in the genomic evolution of a population².

2.1. The role of fossil record in models and reconstructions

In 1971 Lieberman and Crelin made a study that heated the Neandertal question and so began a debate that still endures. From the fossil remains of the specimen from *La Chapelle aux Saints*, the authors reconstructed his larynx in order to verify whether or not that Neadertal had the basics required, from the morphological point of view, to produce the vowels that are typical in modern human phonetics. This model was then compared with the larynx of both modern human newborns and chimpanzees. Their conclusion was that the Neandertal laryngeal structure was more similar to that of a human newborn than to that of an adult human. The possible and impossible sounds for Neandertals are reproduced in Table 3. It is important to keep in mind that within the vowels they could not produce, there are three vowels which are considered universal in modern human phonetics (Maddieson, 1984); additionally, these are the most stable vowels and it is considered the minimal repertoire a language can have: [u], [i], [a]³. The authors

For example, Lieberman (1992) has argued that the kind of "speech" Neandertals held was the genetic factor that provoked their extinction.

Examples of this are the results of several works on Basque population (Alonso *et al.*, 2005; Alzualde *et al.*, 2006), Catalan population from Mallorca descending from Jewish groups (Picornell, *et al.*, 2005), or the Catalan population from Ibiza, the mitocondrial DNA of which could descend directly from Phoenician people (Tomàs, *et al.*, 2006; Zalloua, *et al.*, 2008). These social factors (same language, religion, or even genre) do not work on the genome directly, but they have an influence on mating selection and, hence, indirectly on the future genetic recombinations.

These vowels are the most extreme in the vowel space: [i] is the highest and most anterior, [u] is the highest and most posterior and [a] is the lowest.

argue that modern humans can produce them due to their high larynx position. How is it possible? It is considered in current phonetics that the human vocal system is based on two tubes, two cavities: the first one is horizontal, from the lips to the velum, and a second one is vertical, from the velum to the glotis (see fig. 3)

H. neanderthalensis

	Consonants	Vocals
Impossible	[m], [n], [m], [n], [n], [ŋ], [g], [k]	[u], [i], [a], [ɔ]
Possible	[b], [d], [s], [z], [v], [f]	[I], [e], [U], [x]

Table 3: The Neandertal vocal sounds from Lieberman & Crelin's (1971) model

While in adult humans these two cavities have a similar length, newborns' larynx is higher, so that they cannot emit the same range of sounds. The same happens in chimpanzees, who, on the one hand have a high larynx when compared with humans', and, on the other hand, the horizontal cavity is longer than the vertical one. The most provocative conclusion is that, according to Lieberman & Crelin, the drop of the larynx has not any other adaptive advantage than the benefit for oral communication, while the price is the danger of choking, too high if no compensation makes it bearable.

Later on, Lieberman (1973) has speculated on a evolutionary process in three stages: (1) increase of confidence in vocal communication for activities like hunting; (2) emergence of a vocal tract which is able to produce acoustic signals which are both distinctive and resistant to articulatory errors; (3) evolution of neural mechanisms that made use of the pre-adapted⁴ properties of the supralaryngeal vocal tract for a faster codification of communication. This idea has been redesigned and enhanced through time: it would have been a gradual process that flowed into the current human capacity for voluntarily articulating sounds, which would have been acquired since *H. erectus*⁵ (Lieberman, 1998).

Thus, according to Lieberman & Crelin, the "key factor" of speech evolution would be the specific place where the hyoid bone was placed – a contention criticized by Falk (1975): it was based ona too hihg reconstruction of the hyoid bone position. Falk pointed out that Lieberman & Crelin did not take into account the requirements of "deglutition", nor the age of the subject in relation to the distance of the hyoid bone below the mandible, nor the sexual dimorphism in the development of the thyroid cartilage. Moreover, Falk remarks that, in chimpanzees, the corpus of the hyoid bone "appeared as continuation of

The author makes use of the concept "pre-adaptation", also used by Darwin (1871): "natural selection channeled development in particular directions of previous modifications selected for some other role". This use of the term "pre-adaptation" is not entirely adequate and difers from Darwin's notion, since it should be an *exaptation*. The most important is the idea that follows: in organic evolution there is a continuous exploitation of already existent structures.

Partially in support of this idea, MacLarnon & Hewitt's (1999) conclusions point out that an enhancement of breath control is produced at any point between 1.6 milions of years and 100.000 years ago. Thus, probably in the *H. erectus*'s time.

the laryngeal air sacs⁶" (Falk, 1974, p.125).

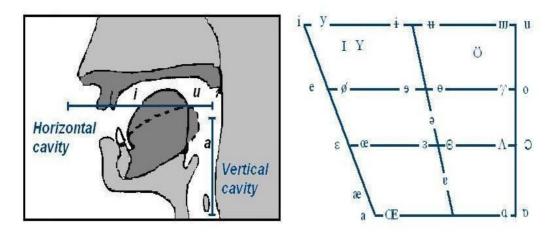


Figure 3: vowels [i], [u], [a], in the human vocal tract (left side) and the repertoire of vowels in human languages (right side).

Thus, the discussion focused on the hyoid bone, quite problematic in fact: it is the only bone of our body which is not in direct touch with another bone, that is to say, it "floats" within tissues. To the incertain position of this bone, a further problem was added up: they had no sample of a hyoid bone of H. neanderthalensis. The debate did not change its course when a Middle Paleolithic hoyid bone – belonging in all probability to a Neandertal individual – was finally found in Kebara (Israel), which had a morphology similar or even identical to that 1989; Bar-Yosef et al.. sapiens (Arensburg *et al.*, Paleoanthropologists were inclined to conclude that this finding supported a lower larynx and hence that speech was already present in H. neanderthalensis. Note how, from the observation of morphological remains, to some extent hazardous conclusions were ventured. This great debate about the linguistic capabilities of Neandertals has often been focused in such a way that sometimes it is not easy to discern whether the object of analysis is language or speech. It has been specially Lieberman who has been centered in doing research into Neadertal speech, and not language⁷ (as cognitive faculty). Lieberman (1993) has rejected these conclusions about the hyoid bone from Kebara, arguing that the shape of the hyoid bone is irrelevant: a pig's hyoid bone could pass for a human's; hence, it does not follow that the shape is linked to a supralaryngeal air duct, since this

This an important observation, because Falk is one of the first in noting the relevance of the laryngeal air sacs in the debate of the evolution of the vocal apparatus. Falk argues that the vertical movement of the hyoid bone "compresses the orifice of the laryngeal air sacs" (p. 125) and hence, this fact also participates in the mechanics when the air sacs are emptied and filled up. Chimps lack of the mechanisms that prevents humans during deglutition, author adds (above all, because they do not need it at all). Next, in the present work, section (2.3.1.) is devoted to laryngeal air sacs, whose absence in human beings has been claimed as one of the apomorphies of the genus *Homo* (see fig. 3).

Though Lieberman has developed an own hypothesis particularly based in speech and how its evolution gave way to the emergence of modern language. On this matter, see below section 4.3.

must not to be linked to the hyoid bone. I partially disagree with Lieberman in this respect: the shape is important because, as we will see next, it points us whether the air sacs were connected to the bone or not, and this fact differentiates us from the rest of great apes (gibbons, gorillas, chimpanzees and bonobos; see below section 4.3.).

Gradually, new morphological elements were introduced which – seemed that – could shed some light and undo the knot that had tied down the debate: the basicranium angle and the hypoglossal canal. Lieberman (1993) has pointed out the relevance of basicranial flexion, a trait that was related to supralaryngeal vocal tract, in which larynx is placed down in the neck. An often unnoticed detail is that this does not mean that Neandertals had no capacity for language or speech, but these would simply be different from ours (Lieberman & Crelin, 1971, p.221). This idea was strengthened with the argument according to which the half of the human tongue remains in the oral cavity, whereas the second half remains into the pharynx. Daniel Lieberman & McCarthy (1999) ousted the use of the basicranium angle as the "key factor", when made a comparison of the ontogeny of this feature in chimps and humans, and finally proved that there is no direct relation between the vertical growth and the vocal tract.



Figure 4: models of H. sapiens (male on the left; female in the middle) and H. neanderthalensis (male on right).

In a letter to *Science*, Lieberman (1999) – against Wolpoff (1998) – disagreed with the physical anthropologist's statements about language in Neandertals based on the hypoglossal canal⁹ (through which the tongue nerves pass). Lieberman (1999) argued that, the fact that chimps cannot talk tells us nothing about the hypoglossal canal¹⁰ (smaller in the genus *Pan* than in the genus *Homo*).

Thus far, it seems that – for the moment – the methodology based on fossil morphological traits only, which could report an articulated vocal capability, is been exhausted. As we have seen, the traditional reconstructions do not let see

This has been admitted by Philip Lieberman (2002, p.555).

In fact, Wolpoff echoed Kay's (1998) work on the hypoglossal canal.

That's the reason why I have not included in this work, as a feature directly related to the capability of vocalization.

either (1) whether or not Neandertals had the required superior vocal space, or (2) whether or not the different components (muscles, bones and cartilages) are located in the proper place they could have when the individual was alive, or (3) whether or not Neandertals were able to manage all this bio-mechanic apparatus in order to produce voluntary vocalizations. Regarding cognition, Krantz (1988) had already speculated that Neandertals had to have some neural circuit which made possible the vocalization *H. sapiens* shows, but the author did not add any detail¹¹. The great problem is how to measure it in Neandertals, when, at best, we can get an endocast of the brain, where one can vaguely detect the brain circumvolutions, verify the lateralization and not much more as regards language¹².

2.2. New approaches for vocalization. The role of larynx

In the last years a great technical development has taken place in the filed of computational models, and this has made possible to face the issue of vocalizations in non-humans from perspectives and techniques different from the above mentioned¹³. Moreover, the tendency to consider the evolution of modern language lightly, disappears practically, in such a way that statements about linguistic capacities from a hyoid bone only, are not abundant any more (though it is often hinted, specially in paleoanthropology).

This notwithstanding, proposals focused on finding "the key factor" of modern speech are still persistent. Such attitude to avoid the creation of a multifactorial model which could integrate different proposals brings, time and time again, to a theoretical cul-de-sac. Now the discussion has addressed the cavities rather than the bones. Making use of new technologies, Honda & Tiede (1998) proposed a new analysis centered in orofacial morphological factors which correlate with the individual variation of the larynx position, measured in a resting condition. Using orofacial geometry, the authors made a statistical analysis that predicts the height of the larynx. Orofacial geometrical data based on magnetic resonance imaging came from previous works (Honda & Tiede 1998; Honda *et al.* 1998). The analyses of correlation showed that the height of the larynx can be predicted either by the aspect ratio of the oral cavity or the antero-posterior dimension of the facial cranium. A concept taken into account in Honda & Tiede

Lieberman (1992), of course, disagreed with that.

This is true regarding the particular cito-architectonic structure that could be involved in Neandertal vocalization. However, there is another kind of information we can get from studies of endocasts and skull shape. For instance, Gunz *et al.* (2010) have proved that both Neandertal and modern human infants had the same brain development in a first stage, but that the latter differs in a second stage, entering in a "globuralization phase" (argued as a derived *H. sapiens* trait). Thus, it seems that both species had the same brain volume at birth and that "most endocranial shape differences develop postnatally". The authors speculate "that a shift way from the ancestral pattern of brain development occurring in early *Homo sapiens* [that is, previous to the Out-of-Africa] underlies brain reorganization and that the associated cognitive differences made this growth pattern a target for positive selection in modern humans." (Gunz *et al.*, 2010, p. R-922)

See de Boer and Fitch (2010) for a historical and critic summary of the computational models of vocal tracts.

(1998) is that of *maximal vowel space*¹⁴. Boë *et al.* (2002) used this parameter as well to estimate the vowel space in Neandertals. Their conclusions are that *H. neanderthalensis* had a vowel space similar to ours and, hence, they could have had the possibility of emitting the same range of vowels, though the authors warn that this does not mean that Neandertals could talk. What they affirm is that the Neandertal had no morphological limitations in this respect. These results have been criticized by Lieberman (2007), who considers that larynx cannot be considered "the key factor" in any case¹⁵; on the contrary, the author proposes that the descent and shape of the tongue is what makes possible to *H. sapiens* the emission of so many different vocalic and consonantic sounds (Lieberman, 2007, p. 556).

The descent of larynx has been indeed an object of attention of many authors; however, sometimes two different debates have been mixed up, when they are essentially different: to have a vowel space like ours does not imply to have a low larynx – like ours – too. The most important difference between Boëand colleagues' and Liberman's arguments is that the former pays attention specially to the relevance of articulatory control, whereas the latter focuses on anatomy. However, the methodology used by Boë et al. (2002) has recently been criticized by de Boer & Fitch (2010), due to the fact that Boë and collaborators' model is based on a previous model – Maeda's (1990) – which is only suitable for modern human speech, de Boer and Fitch argue. The goal of Maeda's model was to determine four points: the jaw's position and the position, shape and tip of the tongue. De Boer and Fitch also note that most animals do not have a L-shaped vocal tract - as we have already seen, essential - exactly as described in the classical source-filter theory. Because Maeda's model cannot report the irregularities of the tongue, its implementation to non-humans can lead to wrong inferences regarding the motor abilities of infants or of non-humans, as according to de Boer and Fitch - in the case of Boë and colleagues. Note in passing, that the same criticism, hence, would be applicable to Lieberman & Crelin's (1971) model. Research based in computational models should be enriched with data from theoretical and field studies, so that the object of study can be outlined with more certainty. A way to do that is introducing the data from the comparative method, as we will see next.

2.2.1. Data from the comparative method. The larynx exaptation.

Currently there is a "new" stream that recovers the concept of exaptation and applies it to the different traits which are related to speech evolution. The descent of larynx, we have seen, cannot be left aside when the human vocal capacity is analyzed. The acoustic consequences are immediate when a mammal has a low or a high larynx. The fact is nonetheless, that it is not "the key factor" that made vocalization possible. On the contrary, it is one change among others – possibly an apomorphy of the genus *Homo* – which has been added to the rest which, as final result – the current one – has produced the current vocalization modern

Boë *et al.*, 2002, p. 473: "n-dimensional space within which are situated the n first formants (resonances) of all possible vocalic sounds that can be realized by a given vocal tract".

This opinion is also shared by Boer & Fitch (2010).

humans exhibit.

The descent of larynx has been explained by Lieberman by means of a functionalist theory: the descent of the larynx was in direct benefit for speech. I disagree, since there are another arguments that look like more convincing, which concern a posterior exaptation of this fact. This kind of argumentation has been put forward by Fitch (2002), while making use of the comparative methodology. Fitch argues that other extant non-human species either can lower the larynx momentarily or even to have it in such position permanently. Within such species - those which have been proven to exhibit a permanent low larynx - we find two kind of deers, the Red deer (Cervus elaphus) and the Fallow deer (Dama dama); the males present a permanent low larynx. This seems to be true for koalas too (Phascolarctos cinereus). The Canidae - for example, dogs - can lower the larynx for a moment. In other words, to exhibit a low larynx is a trait more common in mammals than previously thought. Hence, it should not be so difficult to include Neandertals among them, as Fitch himself has noted 16. The author coincides with Lieberman about the gradual view of such process, but differs from him regarding the function they could have given to it and thinks that the first hominids could have lowered the larynx momentarily (Fitch, 2002, p. 37). Fitch's arguments are based on two facts: (1) this trait is evident in other species, whose males can experiment a second descent of the larynx; (2) given that formants can be used to estimate the size of the emitter, the laryngeal descent could have been favored by the ability to recognize whether the opponent is big or small, or even to make believe the adversary that one is bigger than really is 17.

Thus, while Lieberman and Crelin concede to a descended larynx an adaptive function in order to enhance an articulatory ability – a progressive enhancement of vocalization in genus Homo – Fitch, even when admitting gradual change of the laryngeal morphology, rejects that this has been due to linguistic factors (indeed speech factors); instead, Fitch believes that the quotidian use of the linguistic vocalization is an exaptation of this trait.

This debate has recently been tackled by means of new models: de Boer (2007) created different computational models and then compared the results with real data¹⁸. The results pointed out that an optimal larynx is that whose values are approximately equivalent to the horizontal dimension of the vocal tract (that is to say, as Lieberman has repeatedly said, the values of the horizontal and vertical dimensions are 1:1). The feminine larynx is the one that is closer to the "optimal larynx" – a fact that seems to agree with Lieberman's *et al.* (1969) thesis, according to whom the vocal tract would have evolved in order to be able to offer as many distinctive articulations as possible. Regarding the second descent of larynx in *H. sapiens* males, de Boer finds acceptable the theory about the emitter's size exaggeration (Fitch, 2000) – as the lowest formants point out, and so the

[&]quot;If dogs ca achieve a substantially lowered larynx, without any changes in basicranial angle or hyoid morphology, it seems likely that neanderthals, other fossil hominids or chimpanzees could as well" (Fitch, 2002, p. 34).

This theory is not completely new: Ohala (1984) pointed out that in a lot of human cultures and other non-human species, the F0 is used to look like aggressive and for threatening.

The first, a very simple one, gives the author the values of the "optimal larynx"; the second and third, more realistic, take into account the differences between males and females.

concomitant deeper voice – but the author points out that, even when this moves males away from the "optimal larynx", in no case this supposes a communicative impediment. According to de Boer, the results point out that, if communication is important for surviving, then the larynx which is placed in the best communicative position will be selected.

I would like to stress that during the debate two different issues have been confused: (1) to have an independent articulatory space – as that proposed by Boë et al. (2002) – is independent of the function that a low larynx could have (de Boer, 2007); and (2) to have a particular physical trait does not always imply a particular function. Functions can vary in time. The original function of an organ could have nothing to do with the current function. Fitch (2002) as well as Hauser & Fitch (2003) have noted that the physical part gives us one aspect only of the trait is under analysis – voluntary vocalization with communicative intentions – and hence, the authors affirm that such change, along with important changes in the mechanisms of neuronal control, would have made it smooth for the vocal capacity in *H. sapiens*. In this regard I agree with them and, as I will argue next, this clearly points in two directions: the neuronal aspect (see sections 4.1 and 4.2) and the genes that favor the neuronal control mechanisms in vocal tasks, like *FOXP2* (see section 4.3).

2.2.2. Some conclusions about computational models

The debate about the capabilities for vocalization in Neandertal has been focused until now on morphology, since this was the only secure source of data available at first. The attempts to infer a capacity for oral production counted on little evidences whose argumentation was not difficult to refute. The basicranium angle or the hypoglossal canal alone will never give us more than an trace of how this hominin could have been (traces and signs that must be added up, and not refused, in a global, integrative evolutionary theory of speech). The vocal space in Neandertals seems to be consistent enough in order to produce vocalic sounds, although Boë's et al. (2002) model is more suitable for H. sapiens. Obviously, some species-specific differences are expected, which could move H. neanderthalensis away – at least qualitatively – from H. sapiens. Not in vain, we are talking about two different species. Lieberman's defense against the idea of conceding Neadertals a modern human-like speech, however fierce, does not discard, in my view, the possibilities for a positive conclusion about the Neandertal vowel space, as the new resources and technology seem to point out. Hence, it is conceivable that Neandertals had a superior horizontal vocal tract very similar to that of modern humans, where – although not exactly the same – the potential vowels were very similar to that we nowadays produce. De Boer & Fitch (2010), on the one hand, are pessimistic and think we will never know for sure how the Neandertal vocal tract was. On the other hand, they admit that, even though mammals cannot produce vowels like humans do, it is also true that they could produce enough phonetic distinctions in order to build a basic oral language¹⁹. In effect, this has been proven in other cetacean species (Zoidis et al.,

Of course, the authors refer to the vocalization capability, not to the computational, syntactic aspect that builds human language, an issue they do not go into.

2008) or even primates – being these monkeys (Ouattara *et al.*, 2009a, 2009b) or great apes like orangutans (Spillmann *et al.*, 2010). Thus, voluntary vocalization in general is not an exclusive matter of humans and in this set of species should be included, according to these criteria, the *H. neanderthalensis*. These conclusions are reflected in the following table:

Trait	H. neanderthalensis	H. sapiens	
Low larynx	*		_
Vocal tract	*	$\sqrt{}$	

Table 4: where (*) means "quite possible" and $(\sqrt{})$ means "positive evidence"

Obviously, this does not strictly rule out Lieberman's hypothesis: Neandertals would not have "exactly" the same vocal tract as humans and hence, their vocalizations could perfectly differ from the emitted ones by modern humans. To which extent, it is not possible to verify (for the moment). At the same time, Lieberman's hypothesis does not rule out communication. It is possible that, even in a situation so constrained such the one this author concedes to Neandertals, "smooth" communication could be achieved.

In the next sections I will try to enrich with new pieces of data those aspects that computational models cannot, due to their inherent limitations²⁰. In relation to this question, let me quote de Boer & Fitch's (2010) words about the explanatory scope of computational models of vocal tracts:

"A real vocal tract cannot make all signals that can be produced by a system consisting of two cylindrical tubes, nor can a system consisting of two cylindrical tubes produce all signals that can be produced by a real vocal tract."

(de Boer & Fitch, 2010)

Much the same could be said about other linguistic phenomena like syntax or semantics, in the sense that the models that describe the modern human cannot be good for describing the Neandertal. As a consequence, a strict application of such view would automatically invalidate any kind of inference, even those from the comparative method, making almost impossible to deepen or to offer alternative hypothesis on what has been said about the extinct hominids. However, in the next sections I will show that it is indeed possible to obtain information from other scientific areas, and that such information can be related to *H. neanderthalensis* and its potential vocal capability. These sources, in the line pointed by Fitch (2003), are neuropsychology and genetics. Thanks to the comparative method we will see data from other animals that can help us to draw a picture of the Neandertal phonating capability, richer than that offered by works

As de Boer and Fitch (2010) notice: "The first lesson is that one cannot always apply models and theoretical frameworks that have been developed for modern human language to the evolution of languages and expect valid results".

only based on reconstruction or on simulation. I would like to stress that these works do not have to be excluded, rather on the contrary, they have to be complemented by these new data.

Next and finally ending this part on the vocal tract, I will briefly review the historical evolution of an apomorphy of the genus *Homo*, which distinguishes it from the rest of the *Hominidae* (see fig. 2): the hyoid bone in relation to the lack of laryngeal air sacs. The evolution of these two traits is related with each other and it has had important consequences on the phonating ability of the whole genus *Homo*.

2.3. The hyoid bone in the genus Homo and the missing of air sacs

As I have advanced in section (2.1.), we cannot figure out the evolution of voluntary vocalization from the hyoid bone only. However, it is a good pointer of the phylogenetical path followed by the vocal tract: the hyoid bone has implications in the final result of phonation, and hence, the difference in morphology has to produce (minimal) changes. Falk (1975) said that the critical flaw of Lieberman & Crelin's (1971) results was that the authors had put this bone wrong. Thus, the concomitant result was an unproductive vocal tract in comparison with that of *H. sapiens*. Interestingly, Falk also pointed out the direct relation that this floating bone has with other primates' air sacs of the tribe Hominini, like chimpanzees (Pan troglodytes) and bonobos (Pan paniscus): the hyoid bone compress the orifice of the air sacs. Thus reasonable questions in the sphere of phylogeny of modern human phonetics could be: in which moment has changed the hyoid bone? Is this a change of the whole genus *Homo*, or of the species H. sapiens, or it can even be extendable to the whole subtribe Hominina – see fig. (2) – and hence including Sahelanthropus tchadensis (7 mya), all the Australopithecini (3-4 mya) and the Parathropini?

We find the answer in the fossil record, and this contributes to our knowledge with rather clear data in this case. In this work I assume Wood & Collard's (1999) proposal according to which the genus *Homo* has its birth at the African *H. erectus* clade, also called *H. ergaster*²¹. Thus, when we look at the findings from the fossil record, we see that there is not only a hyoid bone from Kebara ascribable to a Neandertal, as we have already mentioned, but in the Iberian peninsula two more hyoid bones were found (Martínez *et al.*, 2008). Their datation is about 530.000 years and the ascribable species *H. heidelbergensis*. This species is considered a precursor species of Neandertals and of modern humans, though this last issue is more controversial. In any case, if the distribution of the genus *Homo* showed in figure (2) is accepted, the common ancestor of Neandertals and modern humans already had a modern or *derived* hyoid bone.

The authors thus transfer *H. habilis* and *H. rudolfensis* to the genus *Australopitecus* (see fig. 3).



Figure 5: different hyoid bone models from different primates. © Bone Clones www.boneclones.com, with permission.

However, the most important fossil remain that seems to mark the end of an archaic period of the hyoid bone in the subtribe Hominina is the one found in Dikika, Ethiopia (Alemseged et al. 2006) which belongs to an Australopithecus afarensis. The most remarkable characteristic is that the orifice in the corpus clearly reflects the presence of laryngeal air sacs, a trait absent in the hyoid bone of H. heidelbergensis, H. neanderthalensis and H. sapiens. A morphological analysis of the Australopithecus hyoid bone places it in the range of Gorilla gorilla and very close to Pan. This is very interesting from the point of view of the evolutionary history of the vocal tract: hence, it seems that the change of the hyoid bone is linked to the disappearance of the laryngeal air sacs in the genus Homo. If in a near future it is showed that the species currently classified as H. habilis had a primitive hyoid bone like that from Dikika, it could be more forcefully argued that, on the one hand, such species is a member of the genus Australopithecus²² (i.e. Australopithecus habilis); on the other hand, the derived hyoid bone is an apomorphy²³ of the genus *Homo* and that all remaining hominids of this lineage (from H. erectus untill H. sapiens) shared such morphology, much modern and closer to that currently showed by H. sapiens. As we can see in fig. (5), this floating bone has evolved in many different ways in different species. But its effect on modern acoustics begins at the disappearance of air sacs. Next, I will

Much the same could be said, in the case that the hyoid bone is finally found, of *H. floresiensis*: a hominid which presents a lot of morphological features that had been lost at the node of *H. ergaster*. Its inclusion into the genus *Homo* is due to the fact, above all – as in the *H. habilis*' case – that some tools were present in the near of the remains (belonging to the Mode I and some other which belong to the Mode IV), which have been related to that species. Its morphology, however, moves it away from the rest of the members of the genus *Homo*.

²³ See fig. (1).

briefly deal with this morphological trait.

2.3.1. On air sacs

It is indeed intriguing, that a physical trait so evident as laryngeal air sacs has not attracted more attention in the evolutionary studies of linguistics. It is Fitch above all, who has demanded more attention for this apomorphy of the genus *Homo* (Fitch, 2000; Hauser & Fitch 2003): among great apes, only *H. sapiens* has not such organ. This organ has an important effect on vocalizations producing a sound with its own formant. Some species of primates use this sound as a particular call (transcribed as "boom") apparently linked to a particular meaning (Ouattara *et al.*, 2009a, 2009b).

Thus, when, in the lineage *Homo*, did these laryngeal air sacs disappear? Part of the answer has been given in the previous section: the shape of the hyoid bone reveals whether or not a particular species has air sacs. According to what we have seen until now, it is probable that *H. ergaster* already lacked the air sacs, though this remains uncertain, given that no hyoid bone of this species has been found, nor from the precursor, *H. habilis*. What we know for sure is, that the species *H. sapiens*, *H. neanderthalensis* and *H. heidelbergensis*²⁴ showed a "modern" or derived hyoid bone, in the sense that there was no orifice to connect the air sacs.

One could question whether these sacs appeared before or after the emergence of our species. Again, the comparative method and the application of the principle of parsimony give us the key: there are plenty of mammals exhibiting laryngeal air sacs. Among the most representative and related to us, we find the most of primates, but also cetaceans. Studies on both cetaceans (Reidenberg & Laitman, 2008) and primates (Hewitt's *et al.*, 2002) suggest that air sacs are a quite common trait and hence, the most parsymoious conclusion is that, in great apes, the lack of air sacs is a derived trait, and their presence an archaic trait. Given that, among great apes, it is only absent in *H. sapiens*, such novelty can be considered an autapomorphy of this species²⁵.

Apart from that, in relation to the rest of the – extinct – hominids of the genus *Homo* that eventually cohabited with *H. sapiens*, the lack of air sacs is a trait shared with *H. neanderthalensis*²⁶.

Some authors consider *H. heidelbergensis* as just an archaic state of *H. neanderthalensis* and hence, these two species could be gathered in the same species (see Cela-Conde & Ayala, 2001, pp. 336-342). If this is finally confirmed, only two species - and not three - would have confirmed a derived hyoid bone.

It must be noted that there exist a kind of larynegal air sac in *H. sapiens*, but it has a pathological origin: the laryngeal ventricle of Morgani – a little and elliptical cavity located within the false and true vocal folds – can suffer an abnormal saccular dilatation which could expand outside or inside of the larynx. This has been called laryngocele. The increment of air pressure could be its trigger. The most known functional factors are cough, singing or blowing into an instrument (Giovanniello *et al.*, 1970). It is a disease known among trumpet players and glass makers.

And possibly with *H. erectus stricto sensu* (for example, the Asiatic *H. erectus* from Java or from Xina) or even with *H. ergaster* (the African *H. erectus*) – if it is finally confirmed that they coincided in Siberia with Neandertals and Sapiens: recently Krause *et al.* (2010) have

Although in gorillas the morphology is virtually the same, in orangutans it is different. So much differences, as well in primates as in cetaceans, warn us that the functions of these air sacs can be totally different in each species and that probably the primary function they could have will never be known.

Experimental studies using computational models have also dealt with this characteristic physic trait. The results suggest that this organ has a relevant effect on vocalization. Thus, de Boer's (2008) model is inspired in the morphological characteristics of the howler monkey (Aoulatta guariba). The author compared both kinds of productions and obtains very similar results: Whereas howler monkey's vocalizations have peaks around 300, 750 and 1410 Hz, the artificial model reaches 215, 725 and 1215 Hz. De Boer has observed that, when one adds the air sacs to the model, the formants rise getting higher values and new frequencies. This constrains the ability to articulate new sounds. This could be the reason, the author argues, because the air sacs could be lost during the evolution of genus Homo. Riede et al. (2008), in turn, have created several models and their results point to an increase of the variability of the impedance of the vocal tract. Coinciding with de Boer, Riede and collaborators' experiments show that air sacs destabilize the sound source. The authors take into account the data of Siamang (Symphalangus syndactylus) – one of the gibbons (family Hylobatidae), see fig. (2) - who are known to fill the air sacs during the call "boom". Riede and collaborators detect two acoustic effects produced by the air sacs: 1) the air sacs increment the dynamic range of the sound emission, but only the superior and inferior limits; 2) the vocal variability can be incremented in different ways, some of them subject to non-linear and unstable phenomena.

Although it is necessary to make more research in this field, above all, about the functions of the air sacs, some conclusions can be drawn:

- The variety of species in which this organ is present, points us to its antiquity. It is clear that this is a derived trait in extant modern humans shared with Neandertals: both have a derived hyoid bone. Although it is not still sure, there are evidence pointing to the possibility that *H. erectus* already lacked of air sacs and had a derived hyoid bone. However, this has to be confirmed.
- We cannot discard that, in some cases, it could be a case of new and convergent novelty, in other words, a homoplasy (see fig. 1).
- Experiments have stressed the instability effect that air sacs produce and this supports the benefit of maintaining a stable sound source in oral communication, above all in short distances. While air sacs are useful in long distances, as the behavior of Campbell monkeys show, who create a security perimeter around their living area (Ouattara *et al.*, 2009a, 2009b), or the long

published the results of an analysis of DNA of an unknown specimen. It belonged to a hominid for sure, who lived 40k ago in the middle of Siberia, at Denisova. Precisely 100 km faraway from that place, the Teshik-Tash cave (Uzbekistan), in more or less the same time, was inhabited by Neadertals – as Krause's *et al.* (2007) DNA analysis has confirmed. The former species from Denisova has no confirmed species; however, given the fact that the common ancestor of this species, on the one side, and Neandertals and modern humans on the other side, date from 1 mya, it could well be a descendant of an Asiatic *H. erectus*. However, more data is necessary in order to confirm this last suspicion. What seems evident is the fact that before to the exit of *H. sapiens* from Africa, the diversity and co-existence of hominids in some areas was something probable.

vocalizations of orangutans²⁷ – semi-solitary great ape –; these calls seem to be a distortion in short distances. This could be the context that would be favored by the *sudden* disappearance, probably neutral – at least at the beginning –, of the air sacs in the genus *Homo*: close communication within conspecifics.

- The effect caused by laryngeal air sacs does not indicate that the path covered by the genus *Homo* was always the "improvement path" of sound production. Air sacs seem to increment the range of vocalizations: some cercopitecs are known to make use of this organ to emit a particular call (transcribed as "boom"). Nevertheless, I agree with Riede *et al.* (2008) that modern humans are capable of a greater and more refined increment of vocalizations thanks to the multiple combination of articulation points. Note in passing, that this mastery of vocal articulation put for the moment in the same group the whole genus *Homo*, from *H. erectus* till *H. sapiens* (see fig. 3).

In the next table I show two piece of data that we know with certainty regarding the Neandertal and some physical elements of its vocal apparatus:

Trait	H. neanderthalensis	H. sapiens	
Derived hyoid bone	V		
Lack of air sacs	$\sqrt{}$	$\sqrt{}$	

Table 5

3. On the perceptive capabilities of *H. neanderthalensis*

Could the *H. neanderthalensis* recreate the same sounds, and if so, in the same way as modern humans? Firstly, the discussion carried on until now about the vocal space or over the possibility of emitting articulate sounds by Neandertals makes sense only if this hominid was capable of perceiving them as well; or categorizing them as such, in order to produce audible signals.

Sound is a phenomenic experience of our cognition: the information from the auditive organs arrives to particular cerebral regions that convert the neural activity into something perceived as sound. The organ of Corti, in the inner ear, contains the structures that allow the conversion of acoustic stimuli into neural activity.

Next, I will deal with aspects of sound processing that are shared by mammals – for example, formants – in such a way that I'll be able to offer relevant information about the speech processing of Neandertals.

Such vocalizations provide information to orangutans that helps them to confirm the discrimination of males individuals, but also about the context, complemented by the responses of females (Spillmann *et al.*, 2010).

3.1. Formant perception by H. neanderthalensis

An aspect of acoustic processing shared with the rest of mammals is formant perception. This observation was formulated in the 70's by Morton (1977) and was recovered by Fitch (2002). Formants let us differentiate between the vocal sounds we produce, and usually only two formants (F1 and F2) are necessary. In 1969 Lieberman and collaborators already suggested that other mammals could be capable of perceiving formants. In effect, some years latter it has been proven true, at least, in the rhesus macaque – Macaca mulatta – (Hauser et al., 1993), and in vervet monkeys – Chlorocebus aethiops – (Owren, 1990)²⁸. Fitch (2002) holds that formants provide information about the emitter's body size: indeed, several studies seems to corroborate a positive correlation of body size and decreased frequencies in humans, domestic dogs and monkeys (Fitch, 1997; Fitch & Giedd, 1999; Riede & Fitch, 1999). These studies suggest that mammals with a larger body produce lower frequencies. According to Fitch (2002), our mammalian ancestors could have used the frequencies of formants in order to estimate the body size, on the basis of the emitter's vocalizations. Moreover, the author recalls the fundamental role of formant recognition and that most mammals and current birds can discriminate formants. This suggests that the reptilian ancestor of both lineages was also capable of doing it, Fitch adds. With all this in mind, I see no reason to think that Neandertals were not able to do the same and in a similar way to that of *H. sapiens*: the Neandertal man's body was more robust than the anatomically modern human's, but not that robust to create a significative difference regarding formant perception.

The most basic micro-abilities related to speech perception are also under the theoretical scope of *H. neanderthalensis*. There are plenty of data from the comparative method showing that a lot of perceptive micro-abilities, that we link today to language, have their origins millions of years ago (see the cognitive cladogram, in fig. 6): the ability for discriminating between different linguistic rhythmic patterns has been positively proven in five-month-old babies (Nazzi *et al.*, 2000), but also in cotton-top tamarins – *Saguinus oedipus* – (Tincoff *et al.*, 2005), and in common mice – *Mus* – (Toro *et al.*, 2003); categorical perception has been put to the test with positive results in chinchillas – *Chinchilla* – (Kuhl & Miller, 1975).

At Owren's time this species was classified as *Cercopithecus aethiops*.

L. Barceló-Coblijn

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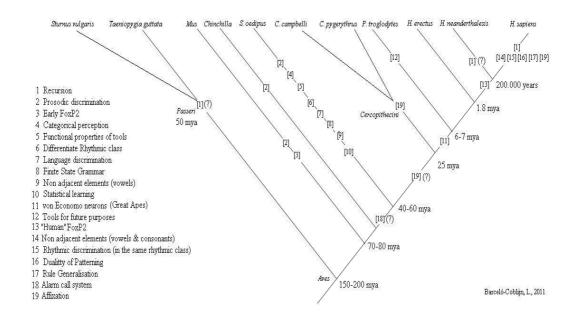


Figure 7: Cognitive cladogram showing traits and abilities proved in other species²⁹.

Therefore, if one pretends to relate these cognitive micro-abilities to that of modern humans and as well as postulating a unique origin, much the same should be applicable to *H. neanderthalensis*.

An aspect I cannot assure for the moment is – pending of improvements in new computational models, or even of new genetic data – which range of frequencies and which combinations could produce this hominid. In this regards, I coincide with the consideration about the fact that the modern human is the extant mammal which can produce the broadest range of formant frequencies (Lieberman *et al.* 1972; Lieberman *et al.* 1969).

Hauser & Fitch (2003) have suggest that another kind of information could be extracted from formants: the speaker's identity. Given the individual differences in the oral and nasal cavities, some subtle differences are produced within speakers, which allows their individual identification. In this sense, it has been suggest that such information could be under the scope of other primates (Rendall *et al.*, 1998) – for example, macaques –, but Hauser and Fitch (2003) consider that there is still not enough information about it, or verifications that allow us to conclude this point. We know that the recognition of a group hierarchy is not an exclusive trait of humans, but also of bonobos and other social mammals (Seyfarth *et al.*, 2005). Identity recognition by means of formants could be important, depending on the species. Although it is still debated the kind of familiar groups predominating in the Neandertal society, it is of general agreement, that this could be a species with a strong social – and possibly also cultural – component (though it is necessary a less broad definition of the concept

A previous version of the cognitive cladogram and the references of the reflected information can be found in Nadal (2009) and in Barceló-Coblijn (in press).

of *culture*). If it is confirmed that this kind of information extraction was already available for hominids before the split between modern humans and Neandertals – as in the case of macaques, above mentioned – it seems that there is no reason to think that a source like that, so useful for social relationships, had fallen from grace in the evolutionary path followed by Neandertals. If the contrary is confirmed, it should be considered the possibility that this is an ability only developed by *H. sapiens* – as regards primates.

From an ethological point of view Ohala (1984) proposed a theory about the use of the fundamental frequency (F0) in aggressive contexts. According to his observations, it seems that when F0 is lower, the voice acquires a "dominant" edge. Curiously enough, the author pointed out that, in humans, high F0 is also used to calm an aggressor, intending not to look like a potential threat³⁰. The author, thus, implicitly supports the positive interpretation by the hearer. Unfortunately, we are still far from knowing how were the formants produced by Neandertals.

3.2. Looking for the auditive bases of H. neanderthalensis

Genetics has contributed enormously in the understanding of species evolution and, in particular, the Neandertal case is maybe one of the most prominent in the last time, given the narrow bond between both hominids and the endless debates surrounding them (this notwithstanding, Neandertals are not always mentioned in works on genetics, from which straightforward inferences can be drawn). In a recent work, carried out by Clark *et al.* (2003), several genes have been detected, which have been target of positive selection during the evolution of mammals – by means of comparison of the genomes of mice, chimps and humans. Regarding the ear and acoustic perception, the authors point to the genes *DIAPH1*, *FOXI1*, *EYA4* and *OTOR*. Some genes of the family *EYA³¹* seem to play a relevant role in the development of eyes and ears; much the same can be said about *FOXI1* (Vidarsson, 2007). The most interesting, however, is that the malfunction in the majority of these genes could produce different kinds of deafness, as we can see in the table 6³².

For the moment, it has not been stated explicitly whether Neandertals had the same variants of these genes exactly. Taking into account the great genetic affinity of both species, it would not be surprising that Neandertals had the same alleles too. This notwithstanding, it should be found out too, whether their expression was exactly the same for Neandertals. Recently, it has been published a work that compiles the last years of genetic research on Neandertals (Green *et al.*, 2010). In the list of genes they include (pp. 714-715), there are all genes that have had a change of amino-acids which are present in current humans, but are ancestral to Neandertals. All of the above mentioned genes are in this provisional list. There also appears the gene *EYA2*, a gene known to interact with the gene

Moreover, Ohala pointed out that this could be a kind of infantile mimicry, and that for obvious reasons natural selection has left most species with a strong inhibition against infanticide.

Whose name comes from "Eyes Absent".

Besides the authors' cited works, the data also comes from *PubMed* > *genes*.

GNAZ. The latter gene has been related to the maintenance of the the ionic balance of perilymphatic and endolymphatic cochlear fluids. Finally, we find a protein linked to the *tectorial membrane*³³, *ALPHA-TECTORIN* (codified by the gene *TECTA*³⁴) whose disruption provokes another form of deafness (Verhoeven *et al.*, 1998).

Gene	Gene ID	Related expression areas	Negative repercussions for the ear and other
DIAPH 1	1729	Regulation of actin polymerization in hair cells of the inner ear.	Autosomal dominant, fully penetrant, nonsyndromic sensorineural progressive low-frequency hearing loss.
FOXI1	2299	Kidney, organ of Corti, epydermis, cochlea and vestibulum.	Human neurosensorial deafness.
EYA4	2070	Organ of Corti.	Postlingual, progressive, autosomal dominant hearing loss at the deafness.
EYA1	2138	Kidney, eye, ear, branquial arches.	Branchiootic syndrome ³⁵
OTOR	56914	Cartilage development and maintenance.	Different forms of deafness

Table 6: Genes related to the inner ear formation and deafness.

Altogether there is firm evidence of the positive selection of some genes related to the ear, to the capacity of auditory perception, and it seems that they have played a fundamental role in the evolution of mammals, in this case in the genus *Homo*. Note, that theirs is not a minor role, in the sense that it affects very basic structures and the most of the times they get expressed in different parts of the body (ear, eye, kidney, etc). Their selection and fixation is not produced suddenly and it would be surprising that Neandertals differed greatly from modern humans regarding these genes; and the fact is that, given the high percentage of genetic similarity and the fact that *introgressive hybridization*³⁶ was possible

An extra cellular matrix of the inner ear that contacts the streocilia bundles of specialized sensory hair cells.

The Gene IDs of *GNAZ* and *TECTA* are 2781 and 7007 respectively.

The hearing loss is variable with respect to severity and age of onset.

We talk about hybridization of two species when the result of such process is a new one species, and the concomitant disappearance of the two precedent species. However, "introgressive hybridization" takes place when two species partially interbreed in such a way that the mechanisms that support the species structure have been violated only occasionally and, hence, the unity of species still endures (in other words, there still remain two species).

(Green *et al.*, 2010); this lead me to think that the individuals descendant of such interbreeding cases were fully biologically viable, in all respects. Otherwise, this little percentage of genes with Neandertal origin would have disappeared from the non African *H. sapiens* populations.

A similar approach to the one that I propose regarding the auditory capabilities of Neandertals, led to Martínez *et al.* (2004) to carry out an experiment, to find out which was the range of sensitivity in kHz of the ear of the hominids from Sima de los Huesos³⁷. The authors created a model from the morphological data from the original skulls, obtained by 3D computerized tomography and recreated the external and inner ear bones too. Their intention was to measure the transmission of the acoustic power. Although what they obtain is not truly an audiogram, one can see a strong correlation with the different frequencies. Martínez and collaborators compared the results from modern humans, chimpanzees and their Atapuerca hominid model. The curve of transmission of acoustic power of the two former differ one from the other clearly, whereas the curve of the Atapuerca hominid model looks like that of modern humans. Moreover, the results place the Atapuerca hominid model sensitivity between 2 and 4 kHz, exactly where *H. sapiens'* sensitivity is located.

3.3. Conclusions about the auditory bases of H. neanderthalensis

Although there will always be some aspects to reinforce, the amount of data is being provided from different study fields always goes in the same direction: the most of aspects and traits that we relate nowadays to perception of modern human's oral language have been inherited in the course of time. Auditory perception, like the visual perception, seems to be a basic structure, of vital importance for mammals, which is not object of frequent or abrupt changes. The Neandertal man, when split off from the group of African hominids and became a separated species, probably was endowed with an auditory perception system very similar or even equal to that of H. sapiens. The genes that have been selected positively since the division of our ancestres suggest such conclusion. Then, the picture of the Neandertal cognition would became more refined than the traditional one that has been offered: the Neandertal man would have not only a physical structure related to vocalization very similar to that of modern humans, but also very similar perceptive auditory capacities, or even alike, including, more over, a set of micro-abilities that seems to be shared by the most of mammals or – in the worst case – by the rest of primates. According to this hypothesis, H. neanderthalensis would have been able - as several mammals - to perceive the formants of sounds; it seems logic that they would also have been capable of extracting information from them, like the emitter's identification or its size. It is not at all clear, however, that Neandertals were capable of manipulating the fundamental frequency in order to look less aggressive, though the contrary, typical in many mammals (humans included), can be attributed to this species. Experimental studies place the auditory sensitivity of Atapuerca hominin (and ancestor of H. neanderthalensis) around 2-4 kHz, precisely the range where

At the Atapuerca Mountains, Burgos, Spain.

Trait	H. neanderthalensis	H. sapiens
Auditory capacity around 2-4 kHz	*	$\sqrt{}$
Formant perception	*	\checkmark
Micro-abilities related to vocalization	*	$\sqrt{}$

human speech is located. These conclusions are reflected in the following table:

Table 6: On the auditory capacities of H. neanderthalensis

Finally, it should be noted that genetics is providing valuable information about the ear, concretely on the genes which seem to have been object of positive selection since the separation of humans from chimps 7 mya. Although we must be cautious regarding the positive evidence of *introgressive hybridization* between Neandertals and Sapiens, the fact of interbreeding points to the possibility that these very genes were shared by Neandertals and modern humans.

4. Some neuronal aspects related to vocalizations

Next, in this section I will talk about neuronal aspects related to vocalization, which, I believe, could be ascribable to Neandertals. This way, I will talk concretely about two kind of neurons (von Economo neurons and mirror neurons) and a gene (FOXP2). I'll try to contribute to the question of Neandertal vocalization showing that it is conceivable that (1) the Neandertal man was endowed with both kinds of neurons and hence this hominid could have been benefited from this neuronal apparatus; (2) that Neandertals had the FOXP2 gene and hence there is room for the possibility for a smooth vocalization ability in this species.

4.1. The von Economo neurons and the Hominidae

Von Economo neurons (VENs) have recently become center-stage given their singularity within great apes and their location, in areas related to vocalization, emotions or facial recognition.

VENs are known long time ago, since their description by Ramon y Cajal himself in 1899 and later by von Economo and Koskinas (1925). Their role is still not well understood, but recently they have attracted attention since Nimchinsky et al. (1999) made the comparative study of this neurons. This kind of neurons are characterized by the shape of their soma, which is not pyramidal, but elongated (spindle shape, indeed³⁸). Their dendritic structure has been described by Watson et al. (2006), who singles out its very reduced number of axons (only two), which are virtually symmetric; additionally, their cellular corpus is up to 4.6 times greater than the rest of (pyramidal) neurons from the layer V. In Nimchinsky's et al, (1999) study, the cerebral tissue of a lot of primate and prosimian species, giving the surprising results that only great apes have this kind of neurons have

In English they are also called *spindle cells*.

been compared. This give us an approximated dating of 15-20 millions of years for their inrush in the history of great apes. Regarding its location, it is concretely the layer V of two areas: the first one, and most important as regards the number of VENs, is the *anterior cingular cortex* (ACC) and the second is the *frontal insula* (FI), with a lower number of such neurons. Watson and collaborators coincide with Nimchinsky *et al.* (1999) when point out that, (1) computationally these neurons are simpler than the pyramidal ones, and (2) their location in the ACC is a sign that they could carry out tasks related with intuition, complex social relationships, vocalization and face recognition.

Cytoarchitecturally, VENs are placed in Brodmann areas 24 and 25. A recent work has discovered, in humans, the presence of VENs in the *disgranular dorsolateral prefrontal cortex*, concretely in the Brodmann area 9 (Fajardo *et al.*, 2008) as it is showed in fig. (8).

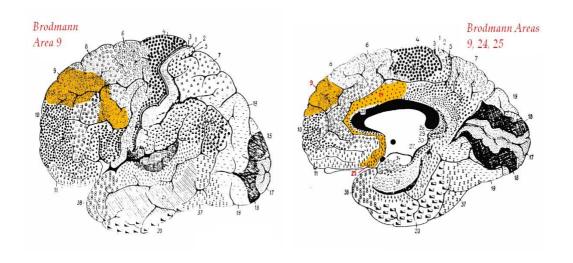


Figure 8: Human cerebral areas where von Economo neurons are located. Picture modified fromWikimedia Commons.

Back to the comparative method, Nimchinsky *et al.* (1999) single out that these kind of neurons are clearly more elongated in chimpanzees and humans than in gorillas and orangutans. The authors conclude that the ACC could have been object of a particular selective pressure (not specified) in the last 15-20 millions of years.

Although previous works singled out the absence of VENs in other mammals³⁹ (among them several cetaceans), it has recently been discovered that VENs are present in the brains of elephants (Hakeem *et al.*, 2005) and in some cetaceans too (Hof & van der Gucht, 2007). Curiously enough, these two groups of mammals coincide with great apes in the use of voluntary vocalizations for communication (for example, the famous whale songs) and in having a rather

In Hof *et al.* (1999), more than thirty mammals from different families: monotremes, marsupials, insectivores, micro- and megachiropterans, rodents, carnivores, artiodactyls and cetaceans.

complex social structure. These coincidences have been considered motives of cellular specialization in these mammals (Hof *et al.*, 2000), that is a case of convergence or homoplasy.

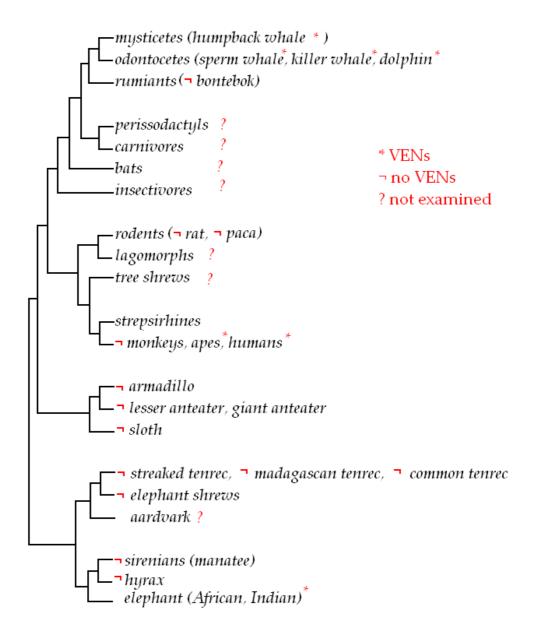


Figure 9: Phylogenetic tree with the species which either have or lack of VENs. Adapted from Haakem et al. (2009)

In relation to the Neandertal man, it is interesting the information that one can extract from the application of the comparative method:

- The species which share this trait - the VENs - are species with a high level of social structure and the use of voluntary vocalizations in communicative

actions. For the moment, no author has posit the presence of VENs as an archaic trait that has survived in the extant species only. On the contrary, the most accepted idea is rather that of an evolutionary convergence based in fitting structural principles. In other words, the morphology of VENs responds to the fact that they are more suitable for specific tasks in specific situations.

– The strong correlation between the encephalization quotient has been put into question by data from pachyderms and cetaceans, though it is still outstanding in the case of great apes. Specially, the distribution of such neurons in bonobos looks like that of humans, being the only two species which have clusters of VENs (Hof *et al.*, 2000). Hence, it seems not so risky to posit that Neandertals also had this kind of neurons, probably in similar number and distribution (to a greater or lesser number) to *H. sapiens*, or between the latter and the bonobo. To posit their absence in Neandertal brains would be counter-intuitive, if we take into account the current data referring the five great apes.

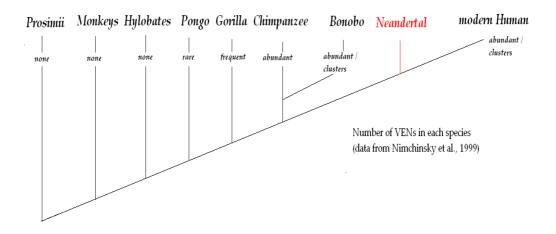


Figure 10: Phylogenetic cladogram and the distribution of VENs in relation to each species

We must note that the role of these neurons is still not well understood, but their physical location provides us with some clues. It is known they have longdistance projections, but their exact connections still remain as a mystery. For the moment, it seems that these neurons are suitable for rapid transmission of information to distant parts of the brain.

Trait	H. neanderthalensis	H. sapiens
Von Economo neurons	*	

Table 7: Von Economo neurons in H. neanderthalensis

Next, I will briefly talk about the ACC and how functions which are attributed to it, like vocalization, can be interesting for the study of the cognitive and vocal capabilities of the Neandertal man.

4.2. The anterior cingular cortex in relation to VENs

The tentative inclusion of VENs in the neuronal landscape of *H. neanderthalensis* opens the door to several interesting research lines. Their presence in the ACC indicates they have a relevant role in activities related to these areas. To the most basic ones like (in the area 24), breathing or cardiac rhythm, others should be added, which are actually related to emotions. The density of the neuronal population at the ACC is indeed low – actually, there is no layer IV in this area –, a fact that makes more conspicuous the presence of VENs in layer V. The area where VENs are placed is curiously the homologous one of an area known to be able to provoke vocalizations with some "meaning" in squirrel monkeys (*Saimiri*) and in the voluntary fonation of macaques (Jürgens & Ploog, 1970; Sutton *et al.*, 1981). We will see that, in spite of the apparent differences between primates, it seems that VENs are not essential for voluntary vocalizing, but they could add emotional content to vocalizations.

Allman *et al.* (2001) have proposed that the ACC is a specialization of the neocortex and not a primitive stadium of cortical evolution⁴⁰ and, moreover, it would participate in intuition or, in pathologic cases, and in autism⁴¹. All this is consistent with what has been argued by Marino *et al.* (2007) about the cognitive abilities of cetaceans. According to these authors, some cetaceans possess a complex brain and their cognition is equally complex, partially supported by VENs, also in layer V of their cetacean brains. Among other already mentioned abilities, there stands out the fact that cetaceans can recognize themselves in a mirror, can vocalize voluntarily and finally they make use of intuition. The two first abilities have also been proven positively in elephants, the other VENs mammal carriers.

All these lead me think that the anterior cingular cortex is related to the production of vocalization with emotional content. If the presence of VENs give us clues about some vocal abilities, the diseases affect them show us the pathological aspect that could affect to some extent vocalization: VENs are specially sensitive to fronto-temporal dementia (Seeley *et al.*, 2006) and to Alzheimer (Nimchinsky, *et al.*, 1995). These diseases affect the three mentioned

To some extent, such conclusions are based in the alleged postnatal emergence of VENs, which was thought to start up the fourth month of postnatal live. However, Hayashi's *et al.* (2001) studies show that VENs appear firstly during the gestation in both humans and chimpanzees (between the weeks 32 and 35). The difference is, that in humans they appear continuously until the forth year of live, whereas in chimps their proliferation downs rapidly in postnatal life.

Besides to the above mentioned capacities, Allman *et al.* (2005) propose a hypothesis about the central role VENs could play in ACC, given that (1) they would be an important part of the circuitry responsible of intuition and (2) they are neurons which become dysfunctional in disorders of autism spectrum. According to this hypothesis, faulty VENs could partially be responsible of the lack of social abilities and this could lead to a lack of intuition.

Brodman areas: 24, 25 and 9. Moreover, lessions in the ACC have been related to a kind of mutism.

If, as the data from genetics and the comparative method suggest, we assume that the brain of the Neandertal man had von Economo neurons at layer V in homologous areas to the above described ones, we have to assume a whole new perspective which goes far beyond that of the "simple" production of categorized sounds. Hence, the picture of *H. neanderthalensis* become very different from that according to which, this hominin was unable even of producing sounds voluntarily or that, in the best case, his vocalizations would only be slightly better than the alarm calls of cercopithecines. On the contrary, according to my approach, it seems that Neandertals could have produced vocalizations with emotional content and, potentially, there could have been cases of mutism within this species due to dysfunction of VENs. We have also seen succinctly – since it is not my goal here – how these neurons could participate in some high cognitive processes and at the same time, in the case of pathologies, how they could be related to diseases of cognition which are traditionally considered of modern human only.

Next, I will analyze the FOXP2 question, a gene that has been linked to the motor control of orofacial muscles, but also to superior order cognitive processes.

4.3. The FOXP2 gene

Twenty years ago Hurst *et al.* (1990) described the disease a British family had – under the pseudonym KE – which affected the 50% of its members. These had speech problems and a kind of verbal dyspraxia was diagnosed. Some years later, the suspicions were confirmed: if three generations show this pathology, its origin must be hereditary.

Enard *et al.* (2002) published a letter in which he announced an analysis of FOXP2, a gene that codifies a protein which belongs to the group of transcription factors called FOX. Enard and his team made sequences of this gene, located at the exon 7q31, and compared it with its ortologous one from a mouse. The authors saw that between *FOXP2* and *FoxP2* there are only three differentiated aminoacids⁴². Such difference is reduced to two different amino-acids when the comparison is made with chimpanzees. Moreover, the authors argue that it must be a fixed gene in the human species, given its low variation among different populations. The rest of primates share the same variant of the gene – the same allele. The modern human the only primate who has a differentiated allele, with changes in two amino-acids The authors dated the gene fixation in modern humans around 200k BP, coinciding more or less with the appearance of *H. sapiens* as species.

Genetic nomenclature can be a little bit confusing:

⁻ When talking about the gene in general, it is written FOXP2.

⁻ When talking about the human variant of the gene (the allele), it is written *FOXP*2, and its protein is FOXP2.

⁻ When talking about the variant of the mouse, it is written *FoxP2* and its protein is FOXP2. More information can be found in HUGO, Guidelines for Human Gene Nomenclature (http://www.genenames.org/guidelines.html#2.%20Gene%20symbols).

The family *KE* has a mutation of this gene⁴³ (Lai *et al.*, 2001). The effects have been related directly to their linguistic deficit in neuroimaging studies, which, when confronted to the results of the affected people with the non-affected people, show different patterns of activation in linguistic tasks: affected individuals have less activity in regions implied with phonological processing (this, according to the authors, would explain the verbal dyspraxia) and in other sub-cortical areas like the basal ganglia^{44,45}.

The exclusivity of this gene in *H. sapiens* finished when Krause *et al.* (2007) accomplished the difficult task of obtaining Neandertal DNA in good conditions⁴⁶ and manage to identify the gene *FOXP2* in the DNA of both Upper Paleolithic hominins. This changes radically the picture: if *H. neanderthalensis* had the same gene with the very same amino-acid substitutions as current modern humans, it could have got the same benefits (and damage) as humans have. More interesting, though, it was the debate (Benítez-Burraco *et al.*, 2008; Coop *et. al.*, 2008) about how it was possible that both hominids shared this gene, when previous results (Green *et al.*, 2006) concluded the contrary. Benítez-Burraco and collaborators (2008) argued that the scenario that would explain the origin of the mutation of *FOXP2* in Neandertals was still not sure, given the little of the sample both Green *et al.* (2006) and Krause *et al.* (2007) counted with. Finally, a very recent publication show some results which seem to confirm that the emergence of this mutation is ancestral in Neandertals, that is to say, it appeared before the division between modern humans and Neandertals (Burbano *et al.*, 2010).

Trait	H. neanderthalensis	H. sapiens
FOXP2		

Table 8: Gene FOXP2 in both hominins

The importance of this gene is not only the fact that it is a derived trait that today shows humans only, but also its implications in motor operations, which aim vocalization. Thus, both *H. neanderthalensis* and *H. sapiens*, before they split

Specifically a conversion $G \to A$. Other patients who were not from family KE had a chromosomal deletion that affects this gene (Feuk *et al.*, 2006; Lennon *et al.*, 2007). In the latter case the symptoms were different, though also within language disorders.

As we will see, this areas are important according to Lieberman's hypothesis, that will be reviewed in section 4.5.

A different kind of vocalization that has been linked to FOXP2 are ultrasounds: oral productions which are produced by air expiration throughout non-vibrating vocal cords. From mouse pups we know that they emit "ultrasonic whistles, clicks and harmonically structured calls of various frequency bandwidths containing varied amounts of noise" (Gaub et al., 2010, p. 391). It is also known that mothers reply to pups (Ehret, 2005). Experiments with mice had pointed out that those individuals with Foxp2-KO (from "knock out"; they are knocked out organisms, created by genetic engineering with inoperative genes) were unable of vocalize ultrasounds (Shu et al., 2005). However, it has recently been published a work that points out that pups could do that in stress conditions (Groszer et al., 2008). Hence, it seems that Foxp2 is not essential for vocalizing ultrasounds (Fisher & Sharff, 2009).

From two individuals found by Rosas *et al.* (2006) in El Sindrón, Asturies.

off, had incorporated a mutation in this gene that made them different from the rest of great apes which did not belong to the genus $Homo^{47}$. The great similarity between both species, however, does not allow us to affirm with certainty whether the expression of FOXP2 was exactly the same in both species. Finally I will recall that there are also problems and mental diseases related with a dysfunction of this gene (diseases that will not be reviewed here due to the scope of the present work): autism (Alarcón *et al.*, 2002; Wassnik *et al.*, 2002) – though very controversial (see Newbury *et al.*, 2002); and schizophrenia (Levy *et al.*, 2010; Sanjuan *et al.*, 2005; Sanjuan *et al.*, 2006). I simply point out that the Neandertal man could have been, thus, a potential subject of such pathologies, in the case that finally is confirmed the supposed role the FOXP2 gene plays therein.

4.4. Mirror neurons and motor theories about language origins

Mirror neurons have been detected in the brain of rhesus macaque (Macaca mulatta) and they are known to fire when the monkey is observing a conspecific grasping an object as well as when the monkey grasp the object itself. When the action consist in grasping something, it is called *transitive* action. When it consists in a similar movement, though without grasping anything, it is called intransitive action. These neurons have still not been detected in H. sapiens brains directly, though there are a considerable amount of indirect data which point to the existence of a mirror neurons system in the human brain, probably very similar to the mirror neurons system of macaques (Stamenov & Gallese, 2002, for a collection of works about this kind of neurons, which also covers other non linguistic issues). The discovering of this kind of neurons along with the indirect data suggesting their existence in modern humans has led to the formulation of a hypothesis about their central role in language evolution (Arbib & Bota, 2003; Arbib 2005, 2006; Rizzolatti & Arbib, 1998). The idea is that this neuronal system help us to understand motor actions like grasping objects and that, in the course of evolution, vocalizations would have been recruited by this system. This theory is supported by the localization of mirror neurons in the macaque, in the so-called F5 area, which seems to be the homologous one of the Brodmann areas 44 and 45, in other words, Broca's area. As we see, the physical location triggers the whole theory: these two Brodmann areas have been related to both motor control and syntax (though the latter is still under discussion). Hence, in the case of hominids, this area would have become specialized and evolved to the current one, in order to favor the perception, control and production of vocalizations. This theory is supported by Corballis (2002a), who argues that it is not happenstance that the motor control and the traditional linguistic areas (Wernicke and Broca's area) are located in the left hemisphere, justifying so the lateralization of language and the difference between both hemispheres (Corballis, 1993). Corballis has affirmed that none of our ancestors – who, as we have seen in the classification of the sub-

I make this specification about the genus *Homo* due to the DNA proofs mentioned above about the mysterious hominid from Denisova (Krause *et al.*, 2010). It is not yet known whether this hominid has the *FoxP2* the chimpanzees show, or the variant shared by Neandertals and modern humans. Current data point to an archaic variant of the gene. In any case, the most recent common ancestor of both hominins should also have the modern version of the gene (being it *H. heidelbergensis* or *H. antencessor*).

tribe *Hominina* (see fig. 3), are many and very different from one another – had more intentional control enough onto bodily movements than to vocalize intentionally (Corballis 2009, p. 27). The same author, in a posterior publication, in the same line of arguments, explains that firstly the gesture was *conventionalized*⁴⁸, and from this point "In the course of human evolution, vocalizations have replaced manual acts as the main medium of language, although manual languages persist, especially in the form of signed languages invented by deaf communities" (Corballis, 2010, p. 28). How this process – in no way trivial or simple – did happen, is not explained. Corballis considers that this change was gradual, almost imperceptible⁴⁹.

4.5. The fitting of Neandertals in the motor theories

Linguistic motor theories assume the difficulty of merging in a whole hypothesis the origin of speech and the origin of language. The principal problem we find in such theories is that they do not take into account the rest of hominids or the rest of species, or only just partially. Rizzolatti & Arbib (1998) argue that a plausible hypothesis would be that the transition from gesture to vocalization has taken place in the transition from the genus Australopithecus to the genus Homo. The first problem comes from paleoanthropology, a discipline which does not ensure that current humans are descendants of australopithecines. Besides this rather intra-theoretical reef, an additional problem is represented by the species H. neanderthalensis. Motor theories of language evolution or on speech evolution have been built onto the basis represented by H. sapiens, partially because the Neandertal man was far from him, regarding cognition and available data. Currently, however, we know that hybridization between anatomically modern humans and Neandertals, although rare and not generally practiced, was possible in a biological sense and, furthermore, not condemned to sterility (Green et al., 2010). Corballis' theory is always based on the argument that H. sapiens were capable of using the mirror neurons system in order to produce controlled voluntary vocalizations. Taking into account all what we have seen, it seems that, on the contrary, we were not the only species of hominins able to do that. It would be quite surprising that, precisely Neandertals – who could potentially have the neuronal and physical elements I have mentioned - were a species of hominin incapable of controlling the vocalizations because they did not reach the mirror system with the alleged incorporation of vocalizations into this system. Differences between Neandertal cognition and H. sapiens cognition are and in fact, there has always been a stream defending such conceivable difference, which would have tipped the balance in favor of the supremacy of the H. sapiens -, in front of the European one - H. African hominin – neanderthalensis. The Neandertal man found in Europe and Asia an ecological niche comfortable enough and occupied this area for almost half a million years. This would have been a period of "cultural stasis" (Ballari et al., 2008). This stasis can be interpreted in two different ways: a) a lack of stimuli or pressures that favor variation, or b) an incapability to develop more complex technology and

Notion borrowed from Burling (1999).

See section 5, on the problems of dating the emergence of speech.

material culture. This issue is currently debated. I just point out, that the differences in cognition should not be due to the lack of mirror neurons, if only because of phylogenetic proximity. However, if, as Corballis has always proposed (2002a, 2002b, 2009a, 2009b, 2010), the transition from the gestural system to the vocal system freed the hands for other tasks, the argument is equally valid for Neandertals, who are known to produce a huge quantity of lithic and other material culture.

In short, I do not find any strong argument to move away *H. neanderthalensis* from the primates with mirror neurons, nor arguments against their potential mastery and use of mirror neurons which, according to Corballis, would have originated language as we find it today in *H. sapiens*.

On the other hand, although the fitting of the Neandertal man in the current Corballis' theory, as it is right now, is difficult without substantial modifications, we can perfectly concede some room for variation in the configuration of the neuronal cables and, specially, variation in the configuration of the mirror neuron system that Neandertal could have had. Then, some differences at that level could certainly have divided both hominins. Not in vain both hominids were phylogenetically separated for hundreds of thousands of years.

Trait	H. neanderthalensis	H. sapiens
Mirror neurons	*	

Table 9

The last of motor theories to consider, is Lieberman's, who argues that the "key factor" in language evolution would be the configuration of the basal ganglia (Lieberman, 2002). As I have already mentioned above, this subcortical structure is affected by the gene *FOXP2*, when it has a mutation like the one of the *KE* family. One notable difference between Lieberman's and Corballis' theory – besides the fact that each author identifies a different element of the cerebral structure as the responsible one – is that Lieberman incorporates the subcortical structures like the basal ganglia, to the already superseded theory on both areas of Wernicke and Broca⁵⁰. Lieberman recalls that an aphasia of Broca – an argument used by Corballis – is never cortical only, but also and necessarily subcortical. Therefore, Lieberman considers that the human capacity for creating motor sequences – vocalizations among them – would have been the basis upon which syntax developed. Enard's *et al.* (2009) experiments show modifications in the neurons that make use of dopamine as neurotransmitter, and in the basal ganglia⁵¹.

Other authors have also pointed out that this duality and localization of the linguistic areas is too simple and that the evidences in neurolinguistics point since long time ago to a net of areas integrated in one system only. Activations in both hemispheres in several linguistic tasks suggest that the model needs a revision and it must be approached from the point of view of complexity; it also seems that this would also be a counterpoint to the most classical theory of modularity of mind. See Stowe *et al.* (2005) for a revision in depth of these questions.

Three kinds of mice are compared: a mouse with its natural FoxP2, a second mouse with the (human) FOXP2 and a third mouse with FOXP2-KO (inoperative gene; see fn. 45).

Lieberman considers that this supports his theory (Lieberman, 2009). However, as in Corballis' or Rizzolatti and Arbib's model, the Neandertal does not fit there. Since this hominin also has the "human" version of the gene and hence, it is expected that its expression would also have affected the basal ganglia of Neandertals, as it affects the basal ganglia of the modern humans and mice. The only argument Lieberman uses against the inclusion of *H. neanderthalensis* in his theory is, in my view, null and void, because it is grounded in the fact that *H. sapiens'* tongue is too elongated for the Neandertal cavity (Lieberman, 2009, p. 802). Instead, he does not offer any argument about why basal ganglia would have not done the same tasks of sequencing in the brain of both hominins.

The great contribution of these motor theories on language evolution is that they furnish us with new data about brain functioning regarding linguistic activities. Moreover, they show us how the brain behaves as an extremely complex machine where the elements interact one with each other. Nevertheless, until these theories do not abandon the strategy of placing both the starting and finish point in the *H. sapiens* species, that is to say, until they integrate the rest of organisms (or at least the closest hominins), these theories will never be complete, because there will always be new data from one or other species, that put into question the alleged specificity of the trait in question (being it mirror neurons or basal ganglia). In my view, none of these theories invalidate the inclusion of the Neandertal within them, rather on the contrary they need it, along with the concomitant modification not only of the theory but also of the perspective they have of the figure of *H. sapiens*, as a virtually extraordinary species (regarding its cognitive capabilities).

5. On the dating of speech

Dating the "emergence" of the vocal tract is something quite difficult because it has been a progressive process and so what we see today as *human speech*. The data regarding the vocal tract and the neuronal apparatus that support it are more conclusive: during the process of *hominization* there has been a continuous stream of changes and exaptations that has flowed into the current vocal tract we have nowadays. If *modern* is linked to *H. sapiens*, then the answer is easy: the emergence itself of this species marks the starting point of this trait (the same could be said of Neandertal "speech"). On the other hand, if *modern* means that it is capable of emitting vocalizations which have previously been analyzed by a system able to put elements in order, sequencing and categorize sounds, then we must be cautious, because other species (not only primates) have some of these aspects as own, and it seems that such species have acquired some of this traits from the ancestors humans and non-humans have in common.

In the same sense, if we refer to vocalization in *H. sapiens*, we have to take into account that many of the factors that intervene therein, have been appearing in the long process of *hominization* and that they could perfectly be shared with other hominids (see fig. 3). To date a gradual process like this is, in the best case, very difficult.

The gradual perspective is coherent with the data that have been found thanks to the comparative method, in such a way that they indicate a previous stadium of philogenetic unity (e.g., the air sacs) or of evolutionary convergence (e.g., von Economo neurons). Hence, in this sense I coincide with Fitch, Lieberman or Corballis, though my approach tries to integrate what we know from different study fields. The coincidences between authors in this respect are few indeed: Lieberman (2007) shows his disagreement with Corballis' (2002) datations, who places 50k BP the emergence not only of modern speech, but also of the grammatical capacity all humans around the world share. In this respect I totally agree with Lieberman when argues that this is simply impossible: the datation of the arrival of humans to Australia – for example, confirmed by studies of mitochondrial DNA (Cann et al., 1983) -, or the artifacts with inscriptions based in geometrical patterns found in South Africa (Henshilwood et al., 2002), confirm that, as it has already been argued in Barceló-Coblijn (in press), we must move back both capabilities to a temporal point previous to the out of Africa. The dates about "the emergence of vocalization" Corballis has made use of, have changed in time: 50k BP (Corballis, 2002b), qualified by Lieberman as "virtually impossible" (Lieberman, 2007, p. 559); 200k – 170k⁵² BP (Corballis, 2009b), this time taking into account Lieberman (1998); finally this author has chosen 170k BP as the most probable dating for the appearance of vocalization (Corballis, 2010). The datations would not be specially relevant but for two reasons: (1) if we talk about a gradual process of biological evolution, how can the limits be established? It is not clear, why should we select a datation, when the trait evolves so slowly and therefore, with very diffused limits; (2) part of the arguments Corballis use, are based on the FOXP2 gene. For this gene, the author sees as more feasible the dating Coop et al. (2008) offer, around 42k BP (the authors argue contamination in Enard's et al., 2002 work). This, as we have already seen when talking about FOXP2, seems not probable, and the last results (Burbano et al., 2010; Green et al., 2010) point to two important facts: a) the dating of the appearance of FOXP2 with two different amino-acids regarding the FoxP2 gene of great apes, would be, at least, previous to the split between H. sapiens and H. neanderthalensis; b) the hybridization, for the moment, has been proven, though, as we have mentioned above, is of the introgressive type; that is, in a punctual moment. This is against Corballis' assumption about the fact that Neandertal would have obtained the *FOXP2* due to interbreeding with *H. sapiens*.

6. Conclusions: on the capabilities for vocalization of *H. neanderthalensis*

In the present work I have gathered several pieces of information from different areas of research, which have a common nexus: all of them tell us something about vocalization. The traits I have analyzed, now gathered in Table 10, show us a richer picture regarding the potential vocal capabilities of Neandertals, than the traditional one, only based in paleomorphic studies or computational studies based in such morphology. In this sense, I have shown how, as claimed by Fitch (2000), the comparative method is a powerful tool in order to infer information, and even more powerful if we can combine it with techniques of genetic analysis, neuronal histologic analysis, or neuroimaging.

In the abstract it says 170.100, probably a misprint.

Trait	H. neanderthalensis	H. sapiens
Low Larynx	*	V
Vocal Tract	*	$\sqrt{}$
Von Economo Neurons	*	$\sqrt{}$
Derived hyoid bone	$\sqrt{}$	$\sqrt{}$
Lack of air sacs	$\sqrt{}$	$\sqrt{}$
Mirror neurons	*	$\sqrt{}$
FOXP2	\checkmark	$\sqrt{}$
Auditory Capacity 2-4 kHz	*	\checkmark
Perception of formants	*	$\sqrt{}$
Micro-abilities related to vocalization	*	\checkmark

Table 10

Looking at Table 10, my conclusion can only be one: current data point to the fact that *H. neanderthalensis* – among all, the phylogenetically closest hominin to *H. sapiens* – had a capability for vocalizations which could be qualified as sophisticated. In effect, not all the traits we see in the table are confirmed, though I think I have shown enough arguments, at least to take them into account for a positive evaluation. It is possible that some doubts will always remain in some cases, but, let me insist, the data from many fields of study lead me believe that all of them were part of the Neandertal man.

Thus, Neandertals would have had a physical structure which would not disable them in order to emit articulate sounds, very similar to that we modern humans produce when talking. Their perceptive capacities seem to go in the same direction: they would have been able to identify sounds, the formants in the case of vocalizations, as it seems that they had a "modern" ear.

A related question is whether or not this species could articulate words as these are understood in the context of the modern human language; whether or not they were able to inflect words or make chains of words until sentences are reached, or produce a derived word from another. None of the proofs shown here point to such a conclusion. I do not think that from a study about the physical and perceptive capacity like this here, one can draw the conclusion that this species already had a syntactic capability or even a morphological capability like that current *H. sapiens* show. I think that these capabilities are essentially bound to computational capacities proven until now in *H. sapiens* only. Noam Chomsky has defended since more than forty years ago, the idea that syntax has a (very powerful) structural component, which allow us to build linguistic structures virtually limitless, which are limited by external components only – like the working memory, or the pulmonary capacity, which are elements that put a "physical" limit to a computational system theoretically so powerful. Such a

computational system, in case of being real, cannot be measured with the data gathered here, though these data can open new research lines.

The goal of this work was to deepen in the biological aspects that seem to support voluntary, articulated vocalization in Neandertals. I have also shown which of them could be attributed to the Neandertal man and to which extent. It will be future research which will confirm some aspects that remain doubtful and maybe also single out new ones, regarding both *H. neanderthalensis* and *H. sapiens*, in order to shed some light onto the biological history of these hominins, and figure out which cognitive differences – if any – separate and distinguish these two hominids.

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