A Biolinguistic Approach to the Vocalizations of *H. Neanderthalensis* and the Genus *Homo*

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This paper revisits the old question about the possibilities and aptitudes *H. neanderthalensis* had for vocalization. New evidence will be discussed 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. An interdisciplinary perspective on the analysis coupled with information gathered from neuropsychology, genetics, and comparative psychology will prove useful for obtaining a new vision in biolinguistics, so that neurocognitive activity becomes important thanks, above all, to the comparison with other species. Finally, it will be argued that it is still plausible to accept the hypothesis on the formation of a vocal capacity prior to the cognitive faculty of language, and independent of it, so that Neandertals were probably able of vocalizing voluntarily, with communicative intentions and in a sophisticated way.

Keywords: air sacs; *Homo (H. neanderthalensis)*; hyoid bone; vocal tract; von Economo neurons

1. Introduction

The issue about language and the communicative possibilities of Neandertals is not new at all. 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. Although this is possible, I argue that, contrary to that first impression and to

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what could apparently be most likely ("what 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* independent from the capacity we humans have to create linguistic constructions that can be conflated to semantic macro-concepts — though it could have co-evolved along with this latter capacity. Our approach takes into account pieces of evidence from several areas of science in an attempt to contribute with a much wider vision than the one we can get exclusively from the hyoid bone. I will apply a quite classic methodology in traditional philology: If one has not got any written proof of a lexical form that could have existed, while at the same time being certain of its existence on the basis of other indirect evidence (e.g., linguistic comparison or reconstruction), then a symbol (*) is applied to the alleged word until a document is found that can prove it. Instead, if one thinks that there is not enough evidence, or that it is not conclusive, a symbol (*X*) will be applied. In the case of a positive conclusion, the symbol will be (√). Let's see some samples not directly related to vocalization:

Trait	**H. neanderthalensis**	**H. sapiens**
Bipedalism	√	√
Chin	X	√
Hyperboreal adaptation[1]	*	X

Table 1: Examples of traits and their evaluation, where (√) means 'positive/present', (X) means 'negative/absent' and (*) means 'probable though not confirmed'.

Thus, we can see how 'bipedalism' is clearly inferable from the osseous morphology. 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, 'hyperboreal adaptation' is clearly absent in modern humans, but not fully rejectable in the case of Neandertals. So I apply an asterisk because there are signs that this is a trait of this species, though 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 Neandertal case. The idea is to draw some conclusions that help me offer a more complete and enriched picture of the issue. Traditionally (and understandably), attention has specially been focused on the analysis of the fossil record, that could reliably indicate a linguistic capacity in this species, so close to *H. Sapiens* from an evolutionary point of view. As we will see, the issue has become more complex than previously thought. Thanks to interdisciplinary work, even some apparently

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[1] This trait refers to an adaptation to cold climates. Thus it is argued that, leaving aside the possibility of using fur covers, Neandertals were somehow adapted to cold regions, as sapiens are to tropical regions. The idea of Neandertal resistance to cold weather has recently been reinforced by the finding of a late Mousterian archaeological site at Byzovaya (Russia) near to the Arctic Circle (Slimak *et al*. 2011). The Mousterian industry has traditionally been linked to Neandertals.

insurmountable obstacles, like the fact that brain does not fossilize, can be overcome in a minimal (but substantial) way. Data from different scientific fields come together in such a way that different areas become linked, so that the issue can be studied from different, but confluent perspectives. In what follows I will also use the comparative method. Comparison between species provides us with clues about what is inferable 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 an extinct species.

The list of the traits that will be object of analysis in the present work is as follows:

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, produced in its source (the larynx), is filtered.
von Economo Neurons	Neurons characterized by its spindle shape and only present in the anterior cingular cortex, in the 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: Traits that have been related to speech and vocalizations

As we can see, traits in Table 2 go well beyond the traditional way to set out the problem of vocalizations in extinct hominids. So, I have bet for interdisciplinary work, importing information from genetics, neuropsychology, and acoustic models. This implies that the physiology of the vocal apparatus loses part of its leading role, favoring an approach that takes into account the role of some brain regions and, more concretely, of some neurons related to particular aspects of human cognition, language and communication. Thus, what matters for vocalization is not just anatomy, 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 around this cavity of the vocal apparatus. So I will consider 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, as well as the possible autapomorphic character of the morphology of this bone in modern humans, as opposed to the rest of great apes. I will also discuss the hyoid bone's orifice where the so-called air sacs are connected, which is lacking in humans but present in all other great apes.

Finally, I contend that vocalization is to a large extent independent of the emergence (in *H. sapiens*) of a capacity until now undetected in other species — I mean a capacity to create meaningful linguistic structures, and to endlessly code thoughts and reflections. Thus, I think there is a clear difference between speech and language, as shown in modern linguistics. Moreover, as a result of my analysis, I will also defend that the critic point in the Neandertal vocalization issue — once theoretically separated from the above mentioned linguistic capacity — is whether or not this hominin had the capabilities for motor control of orofacial and lingual muscular structures and, in the last analysis, the same cognitive capabilities related to linguistic sound processing (i.e. the phonetic and phonological aspects).

1.1. *Some Basic Notions from Evolutionary Studies*

In order to avoid ambiguities, I will use some traditional concepts from cladistics which are useful for describing the characteristics of particular species, particularly specific changes that attract the attention of scientists. Thus, in cladistics (see Kitching *et al*. 1998), a derived change is called *apomorphy.* Whereas adding to it the prefix *sin-* 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. Thus, (i) an example of an autapomorphy is the loss of hair in humans, but not in other primates, (ii) an example of a sinapo-morphy is the loss of hair in cetaceans, but not in other mammals, and (iii) an example of a homoplasy is the fact that both bats and birds have wings.

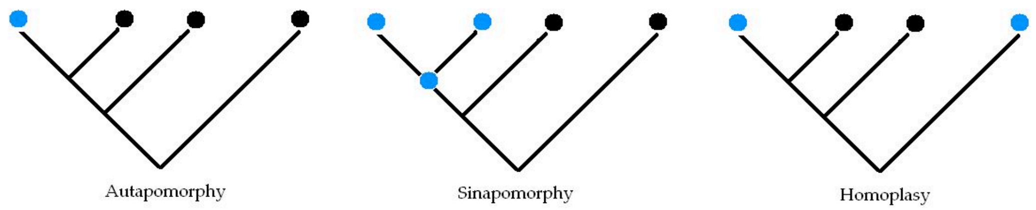

Figure 1: Cladistic concepts

In section 2 I will deal with the perceptive capacity of modern humans which, as it seems, could have co-evolved along with the rest of the vocal apparatus. The reason is that, according to an evolutionary perspective, 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. In this way 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 *H. heidelbergensis*, and, by extension, *H. neanderthalensis*. In doing so we can judge better whether it is a case of autapomorphy, sinapomorphy, or homoplasy.

This methodology is also applied in the third section, where I review some aspects of the neuronal apparatus sustaining part of the human cognition related to speech. 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). Therefore, I am cautious when inferring the presence of certain neurons: on the one hand mirror neurons, and on the other hand *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 constitute a kind of neurons which, from an evolutionary point of view, is very new in primates. In fact, they are present in only one family of hominoids: the *Hominidae* (see Figure 2), which covers the extant species of great apes. These neurons are particularly numerous in the tribe *Hominini* (both genera *Homo* and *Pan*).

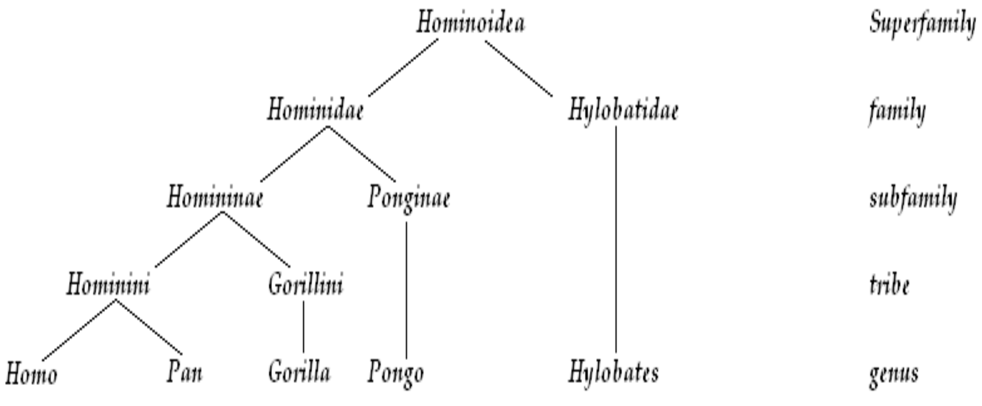

Figure 2: Classification of Hominoidea

The classification of hominids is a burning issue in the current debate of the evolution of human beings. There are many ancestors, and there are several possibilities as to which one of them is our direct precursor. The following classification I is just one among others, and should be taken only as a reference frame, rather than as a firm proposal. However, I have included a mark referring 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 it and, in consequence, it has implications for the conception one could have about a particular fact related to speech.

Finally, the comparative method is also applied at a molecular level. Thus, in the fourth section I will review succinctly the most important aspects of the gene *FOXP2* (and of its protein) as regards the role it plays in vocalization and in the control of orofacial muscles, and other genes related to sound perception as well. This gene is interesting because it is related to some language impairments, but also because the dating of its evolution is quite recent. As a matter of fact, it could be circumscribed to the genus *Homo* or even only to a subset of it.

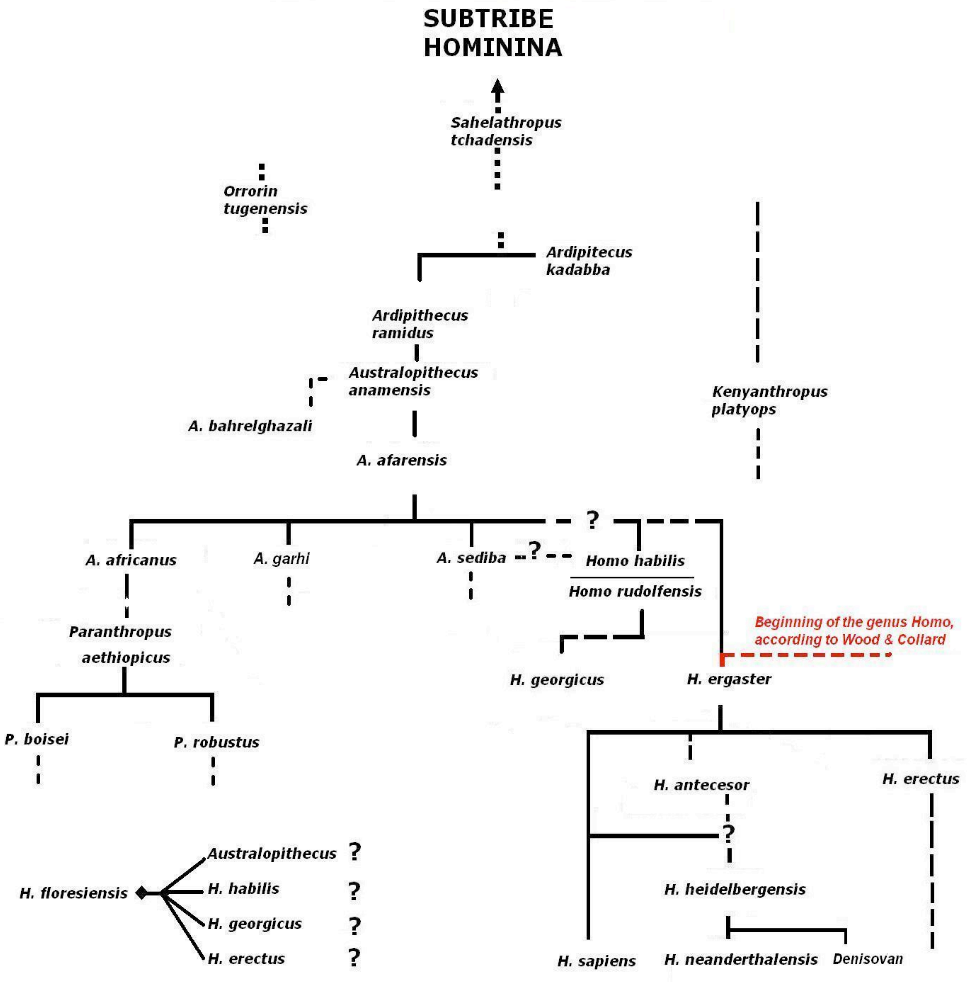

Figure 3: A possible classification of the subtribe Hominina

2. On Vocal Apparatus Reconstructions: The Archaeological Method

The issue of linguistic capacity in species other than *H. sapiens* has been a topic for debate for a long time. Nevertheless, the lack of data sometimes forced 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 unsuitable for scientific research. The discovering of Neandertal remains and its acknowledgement as a species turned out the status of the modern human. This 'cousin' was seen somehow as a kind of 'rival'. The modern human had been considered by many people as the final milestone of evolution. Since then, there has appeared a need to look for the factors that make us humans. One proposed factor was language. This apparently unique human capacity became center-stage in a great debate that still endures nowadays. Language attracted attention in the evolutionary debate, due to its potential explanations of facts still on discussion, like the extinction of Neandertals.[2] Leaving aside the enormous responsibility suddenly acquired by speech concerning the probability of a species survival, Philip Lieberman said something that posterior studies have confirmed — although it is by and large not so radical in their conclusions: In some cases, a language or any other social factor like religion could be an important, if not essential, factor in the genomic evolution of a population.[3]

2.1. *The Role of Fossil Record in Models and Reconstructions*

Lieberman & Crelin (1971) carried out a study that heated the Neandertal issue, and so began a still enduring debate. The authors reconstructed the larynx of the specimen found in *La Chapelle aux Saints* in order to verify whether or not this Neandertal had, from a morphological point of view, the basics required 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. Possible and impossible sounds for Neandertals are reproduced in Table 3. It is important to keep in mind that, among the vowels they could not produce, there are three vowels which are considered universal in modern human phonetics (Maddieson 1984). Furthermore, these are the most stable vowels, so that they are considered the minimal repertoire a language can have: [u], [i], [a].[4] The authors argue that modern humans can produce them due to their high larynx position. How is it possible? According to current phonetics, 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 glottis (see Figure 4).

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[2] For example, Lieberman (1992) has argued that the kind of 'speech' held by Neandertals was the genetic factor that provoked their extinction.

[3] 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, whose mitocondrial DNA could directly descend 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.

[4] 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.

H. neanderthalensis	**Consonants**	**Vocals**
Impossible	[m], [n], [ɱ], [ɲ], [ɳ], [ŋ], [g], [k]	[u], [i], [a], [ɔ]
Possible	[b], [d], [s], [z], [v], [f]	[ɪ], [e], [U], [æ]

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

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

Later on, Lieberman (1973) speculated on an evolutionary process divided 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-adapted[5] properties of the supra-laryngeal 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*[6] (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 on a too high 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 laryngeal air sacs" (Falk 1974: 125).[7]

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[5] The author makes use of the concept 'pre-adaptation', also used by Darwin (1871): "[N]atural 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 differs 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.

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

[7] This is an important observation, since 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.

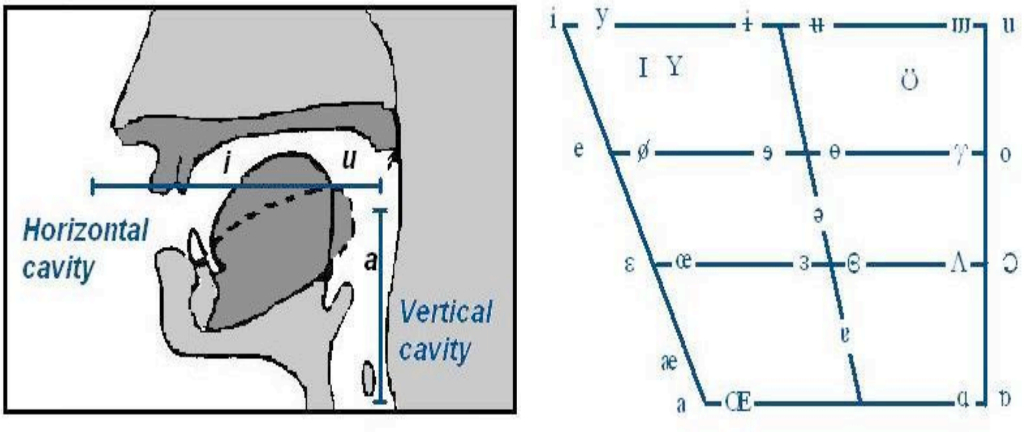

Figure 4: Vowels [i], [u], [a], in the human vocal tract (left side) and the repertoire of vowels in human languages (right side)

Thus, the discussion focused on the hyoid bone, in fact quite problematic: 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 uncertain 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 hyoid bone — belonging in all probability to a Neandertal individual — was finally found at Kebara (Israel). Its morphology was similar or even identical to that of *H. sapiens* (Arensburg *et al*. 1989, Bar-Yosef *et al*. 1992). Paleoanthropologists were inclined to conclude that this finding supported a lower larynx and hence, that speech was already present in *H. neanderthalensis*. It is worth noting that the conclusions ventured from the observation of morphological remains were to some extent hazardous. 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 Neandertal speech, and not language[8] (as a 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 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 helps us decide 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.).

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125) and hence, this fact also participates in the mechanics when the air sacs are emptied and filled up. Chimps lack the mechanisms that prevents humans during deglutition, author adds (above all, because they do not need it at all). Section 2.3.1. of this work is devoted to laryngeal air sacs, whose absence in human beings has been claimed as one of the apomorphies of the genus *Homo* (see Figure 3).

[8] Though Lieberman has developed his own hypothesis particularly based in speech and its evolution paved the way to the emergence of modern language. On this matter, see below section 4.3.

Figure 5: Models of H. sapiens (male on the left; female in the middle) and H. neanderthalensis (male on right)

Gradually, new morphological elements were introduced which could shed some light on the debate and undo the knot that had tied it down: the basicranium angle and the hypoglossal canal. Lieberman (1993) has pointed out the relevance of basicranial flexion, a trait that was related to the 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 only that these would simply be different from ours (Lieberman & Crelin 1971: 221). This idea was strengthened by arguing that while one half of the human tongue remains in the oral cavity, the second half remains into the pharynx. Daniel Lieberman & McCarthy (1999) ousted the use of the basicranium angle as the 'key factor', when they compared the ontogeny of this feature in chimps and humans, and proved that there is no direct relation between the vertical growth and the vocal tract.[9]

In a letter to *Science*, Lieberman (1999) — against Wolpoff (1998) — disagreed with the physical anthropologists's statements which base the presence of language in Neandertals on their having the hypoglossal canal[10] (through which the tongue nerves pass). Lieberman (1999) argued that, the fact that chimps cannot talk tells us nothing about the hypoglossal canal[11] (smaller in the genus *Pan* than in the genus *Homo*).

Thus it seems that — for the moment — the methodology pretending to report an articulated vocal capability based only on fossil morphological traits, has been exhausted. As we have seen, the traditional reconstructions do not let see 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 properly in the place they had in living individuals, or (3) whether or not Neandertals were able to manage all this bio-mechanic apparatus in order to produce voluntary vocalizations. As far as cognition is concerned, Krantz (1988) had already speculated that Neandertals had to have some neural circuit which made possible the vocalization exhibited by *H. sapiens*, but he did not add any

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[9] This has been admitted by Philip Lieberman (2002: 555).

[10] In fact, Wolpoff echoed the work made by Kay *et al.* (1998) on the hypoglossal canal.

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

detail.[12] The great problem is how to measure it in Neandertals, when the best we can get is an endocast of the brain, where one can vaguely detect the brain's circumvolutions, verify the lateralization and not much more as regards language.[13]

2.2. *New Approaches for Vocalization: The Role of Larynx*

In recent years a great technical development has taken place in the field of computational models. This has allowed facing the issue of vocalizations in non-humans from perspectives and techniques which differ from the aforementioned.[14] Moreover, the tendency to consider the evolution of modern language lightly practically disappears, so that statements about linguistic capacities based only on the presence of the hyoid bone are not frequent any more (though they are often hinted, especially in paleoanthropology).

This notwithstanding, proposals focused on finding the 'key factor' of modern speech are still persistent. Such tendency to avoid the creation of a multi-factorial model which could integrate different proposals brings, time and time again, to a theoretical cul-de-sac. Now the discussion has moved to cavities rather than to 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, Tiede, 1998). The analyses of correlation showed that the height of the larynx can be predicted either from the aspect ratio of the oral cavity or from the antero-posterior dimension of the facial cranium. A concept taken into account in Honda & Tiede (1998) is that of *maximal vowel space*.[15] Boë *et al*. (2002) used this parameter to estimate the vowel space in Neandertals. They concluded *H. neanderthalensis* had a vowel space similar to ours and, hence, could have been able to emit the same range of vowels, though they warned that this does not mean that Neandertals were able to talk. What they affirm is that Neandertals had no morphological limitations in this respect. These results have been criticized by Lieberman (2007), who consi-

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[12] Lieberman (1992), of course, would disagree with that.

[13] 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 differ in a second stage, entering 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 away 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: R-922)

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

[15] Boë *et al*. (2002: 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".

ders that larynx cannot be considered the 'key factor' in any case;[16] 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 consonantal sounds (Lieberman 2007: 556).

Indeed, many authors have paid attention to the descent of larynx. However, sometimes two different debates have been mixed up, when they are essentially different: Having a *vowel space* like ours does not imply to have a low larynx like ours too. The most important difference between Boë and colleagues, on one side, and Liberman's arguments, on the other, is that the former pays special attention to the relevance of articulatory control, whereas the latter focuses on anatomy. However, the methodology used by Boë *et al.* (2002) has been recently criticized by de Boer & Fitch (2010), due to the fact that the model of Boë and his collaborators is based on a previous model — Maeda's (1990). De Boer & Fitch argue that this model is suitable only for modern human speech. 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 an L-shaped vocal tract — something essential, as we have seen — exactly as described in the classical *source-filter* theory. De Boer & Fitch add that, since Maeda's model cannot report the irregularities of the tongue, its application to non-humans can lead to wrong inferences regarding the motor abilities of infants or of non-humans, as 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. Introducing the data from the comparative method is a way to do that, as we will see next.

2.2.1. *Data from the Comparative Method: The Larynx Exaptation*

Nowadays there is a 'new' trend which recovers the concept of *exaptation* and applies it to the different traits involved in speech evolution. We have seen that the descent of larynx cannot be left aside when one analyzes the human vocal capacity. The fact that a mammal has a low or a high larynx has immediate acoustic consequences. Nonetheless, it is not the 'key factor' that made vocalizing possible. On the contrary, it is one change among others — possibly an apomorphy of the genus *Homo* — which has been added to the rest.

The descent of larynx has been explained by Lieberman by means of a functionalist theory: The descent of the larynx was beneficial to speech. I disagree with this view, since there are other, more convincing, arguments, concerning a posterior exaptation of this fact. This kind of argumentation has been put forward by Fitch (2002) using the comparative methodology. Fitch argues that other extant non-human species can either lower the larynx momentarily or even maintain it in such a position permanently. Within those that have been proven to exhibit a permanent low larynx, we find two kinds of deers, the Red deer (*Cervus elaphus*) and the Fallow deer (*Dama dama*); the males present a permanent

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

low larynx. This seems to be also true for koalas (*Phascolarctos cinereus*). *Canidae* — for example, dogs — can lower the larynx for a moment. In other words, the exhibition of 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.[17] The author coincides with Lieberman about the gradual view of such a 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: 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.[18]

Thus, while Lieberman & Crelin concede the descended larynx an adaptive function enhancing an articulatory ability — a progressive enhancement of vocalization in genus *Homo* —, Fitch, even admitting gradual change of the laryngeal morphology, rejects that this has been due to linguistic factors (concretely, 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 data.[19] 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, that 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 *et al.*'s (1969) thesis that the vocal tract would have evolved in order to enable as many distinctive articulations as possible. Regarding the second descent of larynx in *H. sapiens* males, de Boer accepts the theory about the emitter's size exaggeration (Fitch, 2000) — as the lowest formants point out-, and so the concomitant deeper voice. But he points out that, although this moves males away from the 'optimal larynx', in no way supposes a communicative impediment. According to de Boer, the results suggest 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 two different issues have been confused during the debate: (1) to have an independent articulatory space — as that proposed by Boë *et al.* (2002) — is independent of the function 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 only one aspect

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[17] "If dogs can 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: 34).

[18] 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 seem aggressive and for threatening.

[19] 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.

of the trait under analysis — voluntary vocalization with communicative intentions — and hence, the authors affirm that such a change, along with other important changes in the mechanisms of neuronal control, would have smoothed the path 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 at first available. 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 a trace of how this hominin could have been (traces and signs that must be *added up*, and not refused, into 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 *et al.*'s (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 for nothing are we talking about two species. Lieberman's defense against the idea of conceding Neadertals a modern human-like speech, however fierce, does not discard the possibilities for a positive conclusion about the Neandertal vowel space, as the newly available resources and technology seem to point out (Boë *et al*. 2002, 2004, Fitch 2002). Hence, it is conceivable a Neandertals superior horizontal vocal tract very similar to that of modern humans, in which the potential vowels would have been very similar — if not exactly the same- to that we produce nowadays. De Boer & Fitch (2010), on the one hand, are pessimistic and think we will never know for sure how the Neandertal vocal tract was. Nonetheless, 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 language.[20] In effect, this has been proven in other cetacean species (Zoidis *et al*. 2008) or even primates — be these monkeys (Ouattara *et al*. 2009a, b) or great apes like orangutans (Spillmann *et al*. 2010). Thus, voluntary vocalization in general is not an exclusive matter of humans and the *H. Neanderthalensis* should be included, according to these criteria, in this set of species. These conclusions are reflected in the following table:

Trait	***H. neanderthalensis***	***H. sapiens***
Low larynx	*	√
Vocal tract	*	√

Table 4: Probably Neandertals had a similar laryxn and vocal tract

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[20] 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.

Obviously, this does not rule out strictly Lieberman's hypothesis: Neandertals would not have 'exactly' the same vocal tract as humans and hence their vocalizations could perfectly differ from ours. To which extent, it is still not possible to verify. At the same time, Lieberman's hypothesis does not rule out communication. It is possible that, even in a situation so constrained as the one this author assigns 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 deal with, due to their inherent limitations.[21] Regarding 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 a view would automatically invalidate any kind of inference, even those from the comparative method, making almost impossible to deepen the hypothesis on what has been said about the extinct hominids or to offer alternative ones. However, I will show in the next sections 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 only based on reconstruction or on simulation. I would like to stress that these works do not have to be excluded. On the contrary, they have rather 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 Figure 3): the hyoid bone in relation to the lack of laryngeal air sacs. The fact that these two traits are evolutionary related to each other 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 only from the hyoid bone. 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, this being, the difference in

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[21] As de Boer & 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" (p. 15 of the pre-publication manuscript).

morphology has to produce (minimal) changes. Falk (1975) said that the critical flaw in Lieberman & Crelin's (1971) results was that the authors had wrongly placed this bone. Thus, the concomitant result was an unproductive vocal tract in comparison with that of *H. sapiens*. Interestingly, Falk also pointed out the direct relation of this floating bone with other primates' air sacs of the tribe *Hominini*, like chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*): the hyoid bone compresses the orifice of the air sacs. Thus, one may ask some reasonable questions: in which moment has changed the hyoid bone? Is this a change of the whole genus *Homo*, or just of the species *H. sapiens*? Can it be extendable even to the whole subtribe *Hominina* described in Figure 3?

We find the answer in the fossil record. As said, 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*.[22] I'll show that the hyoid bone is another trait in favor of this classification.

Additional to the Neandertal hyoid bone from Kebara, two more hyoid bones were found in the Iberian peninsula (Martínez *et al*. 2008). They date from about 530.000 years and belong to the *H. Heidelbergensis*, species, considered a precursor of both Neandertals and modern humans (Mounier *et al*. 2011), though this last issue is more controversial.[23] Anyway, if a distribution as the one showed in Figure 2 is accepted, the common ancestor of Neandertals and modern humans already had a modern or *derived* hyoid bone.

Figure 6: Different hyoid bone models from different primates. © Bone Clones www.boneclones.com, with permission

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[22] These authors thus transfer *H. habilis* and *H. rudolfensis* to the genus *Australopitecus* (see Figure 3).

[23] *Homo heidelbergensis* has also been called *archaic Homo sapiens*. Other authors consider *H. heidelbergensis* just an archaic state of *H. neanderthalensis* and hence, these two species could be merged into the same species (see Cela-Conde & Ayala 2001: 336–342). If this is finally confirmed, only two species and not three would have confirmed a derived hyoid bone.

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 at 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 *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*.[24] This floating bone has evolved in many different ways in different species (Figure 6). But its effect on modern acoustics begins with the disappearance of air sacs.

Laryngeal air sacs have been almost unnoticed by scholars. 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* lacks them. Air sacs have an important effect on vocalizations, producing a sound with its own formant. Campbell's monkeys use this sound as a particular call apparently linked to a particular meaning (Ouattara *et al.* 2009a, b).

One could question whether or not these sacs appeared previously to the emergence of our species. Again, I apply the *principle of parsimony*: There are plenty of mammals exhibiting laryngeal air sacs, like primates, but also cetaceans (Reidenberg & Laitman 2008, Hewitt *et al.* 2002) which suggests that air sacs are a quite common ancient trait. Within great apes such novelty can be considered an autapomorphy of *H. sapiens*.[25]

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]

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[24] If in the future it is shown that the species currently classified as *H. habilis* had a primitive hyoid bone like that from Dikika, it could be more forcefully argued (1) thar such species is a member of the genus *Australopithecus (i.e. Australopithecus habilis); (2)* that the derived hyoid bone is an apomorphy of the genus Homo and (3) that all remaining hominids of this lineage (from *H. erectus till H. sapiens*) shared such morphology, much modern and closer to that shown by *H. sapiens.* Much the same could be said, of *H. floresiensis*: a hominid which presents several morphological features that had been lost at the node of *H. ergaster.* Its inclusion into the genus *Homo* is due to the fact — as in the *H. habilis'* case — that some tools were present in the near of the remains (some of them belonging to the Mode I and some other to the Mode IV), relating them to that species. Its morphology, however, moves it away from the rest of the members of the genus *Homo.*

[25] Note that there exists a kind of laryngeal 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 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.

[26] And probably with another new species: Recently Krause *et al.* (2010) have published the results of an analysis of DNA of an unknown specimen dubbed the 'Denisovian hominid'. It is for sure a hominid, and lived 40k ago in the middle of Siberia, at the Denisova cave. Precisely 100 km far away from that place, the Teshik-Tash cave (Uzbekistan), at more or less the same time, was inhabited by Neandertals — as Krause *et al.*'s (2007) DNA analysis has confirmed.

A first datation suggested that the common ancestor of Denisovians on the one side, and Neandertals and modern humans on the other side, dated from 1 mya, and hence it could well be a descendant of an Asiatic *H. erectus*. Nonetheless, two recent works have shown

Experimental studies using computational models have also dealt with this characteristic physical trait and have found that air sacs affect vocalic formants elevating them and thus loosing vocalic space (de Boer 2008, Riede *et al.* 2008). Although it is necessary to make more research in this field, especially on the functions of air sacs, some conclusions can be drawn. First, the variety of species having this organ suggests us its ancient character. Its absence is a derived trait in extant modern humans, shared with Neandertals. Though it should be confirmed, the evidence points to the possibility that *H. erectus* already lacked air sacs and also had a derived hyoid bone.

Second, we cannot discard that in some cases it could be a case of new and convergent novelty or *homoplasy* (see Figure 1).

Third, experiments have stressed the instability effect produced by air sacs 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 shown by the behavior of Campbell's monkeys, who create a security perimeter around their living area (Ouattara *et al.* 2009a, b), or by the long vocalizations of orangutans[27] — semi-solitary great apes — whose calls seem to be a distortion source in short distances. This could be the context that would be favored by the *sudden* disappearance, probably neutral in a first moment, of the air sacs in the genus *Homo*: close communication within con-specifics.

Lastly, 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 ('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 would put for the moment into the same group the whole genus *Homo*, from *H. erectus* till *H. sapiens* (see Figure 3).

In the next table I show two pieces of data that we unquestionably know regarding the Neandertal man:

Trait	***H. neanderthalensis***	***H. sapiens***
Derived hyoid bone	√	√
Lack of air sacs	√	√

Table 5: Both species show a derived hyoid bone

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that (1) Denisovians were closer to Neandertals than to Sapiens, and (2) that Denisovians interbreed with the Sapiens that reached southeast Asia and Oceania (Reich *et al*. 2011, Vorobieva *et al*. 2011). What seems evident is the fact that the diversity and co-existence of hominids in some areas was something usual before the exit of *H. sapiens* from Africa.

[27] Such vocalizations provide information to orangutans helping them to confirm the discrimination of male individuals, but also information on the context, complemented by the responses of females (Spillmann *et al*. 2010).

3. On the Perceptive Capabilities of *H. Neanderthalensis*

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 and processing them as we do: categorizing them linguistically, in order to reproduce them later on as audible signals. Could the *H. neanderthalensis* recreate the same sounds, and if so, in the same way as modern humans?

Sound is a phenomenic experience of our cognition: The information from the auditory organs arrives to particular cerebral regions that transform 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.

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 recovered by Fitch (2002). Formants let us differentiate between vocal sounds, and in normal conditions only two formants (F1 and F2) are necessary. In 1969 Lieberman and collaborators already suggested that other non-human mammals could be able of perceiving formants. In effect, some years later it has been proven true in rhesus macaque (*Macaca mulatta*; Hauser *et al.* 1993) and vervet monkeys (*Chlorocebus aethiops*; Owren 1990).[28] Fitch (2002) holds that formants provide information about the emitter's body size: Indeed, several studies seem 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 reminds us the fundamental role of formant recognition and the fact that most mammals and current birds can discriminate formants. According to Fitch, this suggests that the reptilian ancestor of both lineages was also capable of doing it. With all this in mind, I see no reason to think that Neandertals were not able to do the same as *H. Sapiens* and this in a similar way: The Neandertal man's body was more robust than the anatomically modern human's, but not so robust as to create a signifycant difference regarding formant perception.

The most basic micro-abilities related to speech perception are theoretically also available to *H. neanderthalensis*. There are plenty of data from the comparative method showing that a lot of perceptive micro-abilities we link today to language have their origins millions of years ago (see the cognitive cladogram in

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[28] This species was classified as *Cercopithecus aethiops* at Owren's time and still is today.

Figure 6): The ability to discriminate 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).

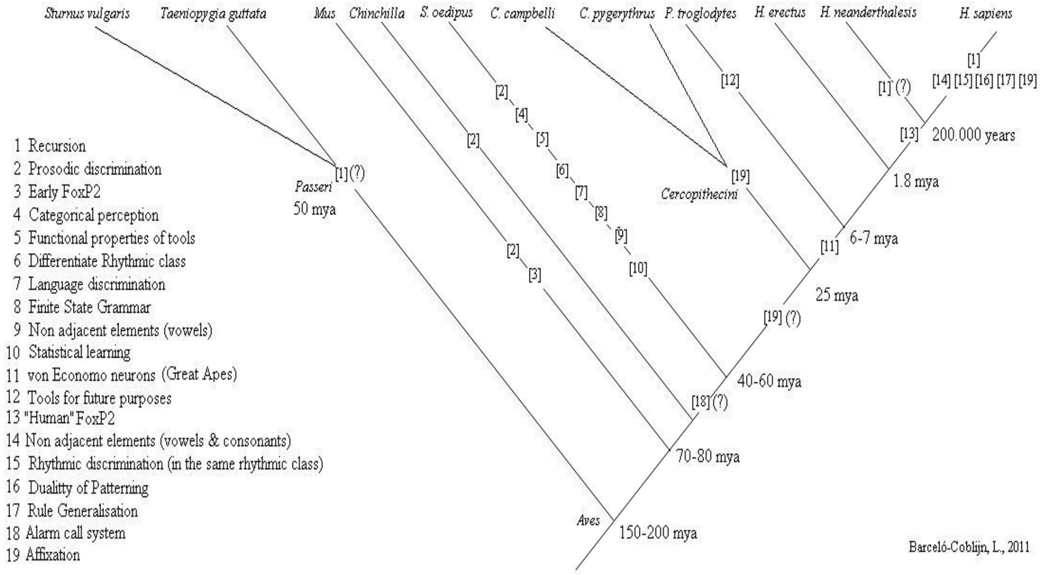

Figure 7: Cognitive cladogram showing traits and abilities proved in other species[29]

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

An aspect I cannot assure for the moment (pending improvements in new computational models, or even of new genetic data) is which range of frequencies and which combinations this hominid could produce. In this regard, 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, 1969).

Hauser & Fitch (2003) have suggested 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 allow their individual identification. In this sense, it has been suggested that such information could be within the scope of other primates (for example, macaques; Rendall *et al.* 1998), but Hauser & Fitch (2003) consider that there is still not enough information about it, or verifications that allow us to conclude anything on this point. We know that the recognition of group hierarchy is not an exclusive trait of humans, but also of bonobos and other social

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[29] Previous versions of the cognitive cladogram and the references of traits can be found in Nadal (2009) and in Barceló-Coblijn (in press). The cognitive cladogram evolves parallel to research on animal cognition.

mammals (Seyfarth *et al.* 2005). Identity recognition by means of formants could be important, depending on the species. Although it is still debated what kind of familiar groups were predominant in the Neandertal society, it is generally agreed that this species could count on a strong social — and possibly also cultural — component (though it would be necessary a less broad definition of the concept 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, mentioned above), 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* — but not by the rest of primates.

Ohala (1984) proposed a theory, from an ethological point of view, 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, a high F0 is also used to calm an aggressor, trying not to look like a potential threat.[30] Thus, the author implicitly supports the positive interpretation by the hearer. Unfortunately, we are still far from knowing how the formants were produced by Neandertals.

3.2. Looking for the Auditory Bases of H. Neanderthalensis

Genetics has contributed enormously to the understanding of species evolution. In particular, maybe the Neandertal case is one of the most prominent in recent t times, 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, Clark *et al.* (2003) have detected several genes which have been the 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 *EYA* family[31] seem to play a relevant role in the development of eyes and ears; much the same can be said about *FOXI1* (Vidarsson 2007). Most interesting, however, is the fact that the malfunction in the majority of these genes could produce different kinds of deafness, as we can see in Table 6.[32]

For the moment, it has not been stated explicitly whether Neandertals had exactly the same variants of these genes. Taking into account the great genetic affinity of both species, it would not be surprising that Neandertals had also the same alleles. This notwithstanding, it should also be found out whether their expression was exactly the same for Neandertals. A work compiling the last years

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[30] Interestingly, 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.

[31] Whose name comes from 'Eyes Absent'.

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

of genetic research on Neandertals has been published recently (Green *et al.* 2010). In the included list of genes (pp. 714f.), 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 *GNAZ*. The latter gene has been related to the maintenance of 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*
DIAPH1	*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 most of the time 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. The fact is that, given the high percentage of genetic similarity and the fact that *introgressive hybridization*[36] was possible (Green *et al.* 2010), one must contend that the individuals descendant of

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

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

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

[36] 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).

such interbreeding cases were in all respects fully biologically viable. 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 I propose regarding the auditory capabilities of Neandertals, led to Martínez *et al*. (2004) to carry out an experiment in order to find out which was the range of sensitivity in kHz of the ear of the hominids from Sima de los Huesos.[37] The authors created a model taking into account the morphological data from the original skulls, obtained by 3D computerized tomography. They also recreated the external and inner ear bones. Their intention was to measure the transmission of the acoustic power. Although what they obtained is not a true 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 in the two former cases differs 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 strengthen, the amount of data being provided from different fields of study always point to the same direction: Most aspects and traits nowadays related to the perception of modern human's oral language have been inherited in the course of time. Auditory perception, like visual perception, seems to be a vitally important basic structure for mammals, which is not subjected to frequent or abrupt changes. The Neandertal man, when split off from the group of African hominids, becoming 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 ancestors on the one hand and the comparative method results on the other hand, suggest such parsimonious conclusion. Then, the picture of the Neandertal cognition would became more refined than the traditionally offered one: The Neandertal man would have not only a physical structure related to vocalization very similar to that of modern humans, but also very similar, or even identical, perceptive auditory capacities, including, moreover, a set of micro-abilities that seems to be shared by most mammals or — in the worst of cases — by the rest of primates. According to this hypothesis, *H. neanderthalensis* would have been able 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, 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 human speech is located. These conclusions are reflected in the following table:

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[37] At the Atapuerca Mountains, Burgos, Spain.

Trait	***H. neanderthalensis***	***H. sapiens***
Auditory capacity around 2-4 kHz	*	√
Formant perception	*	√
Micro-abilities related to vocalization	*	√

Table 7: On the auditory capacities of H. *neanderthalensis*

Finally, it should be noted that genetics is providing valuable information on 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 proved interbreeding suggest the possibility that these genes were shared by Neandertals and modern humans (and Denisovians, for that matters).

4. Some Neuronal Aspects Related to Vocalizations

Next, in this section, I will talk about neuronal aspects related to vocalization, which could be ascribable to Neandertals. More concretely, I will talk about two kinds of neurons (von Economo neurons and mirror neurons) and one 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 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 have been known for a long time, since their description by Ramon y Cajal himself in 1899 and later on by von Economo & Koskinas (1925). Their role is still not well understood, but recently they have attracted attention, since Nimchinsky *et al.* (1999) made a comparative study of these neurons. This kind of neurons is characterized by the shape of their soma, which is not pyramidal, but elongated (spindle shape, indeed[38]). 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. Nimchinsky *et al.*'s (1999) study of the cerebral tissue of a lot of primate and prosimian species provides the surprising results that only great apes have this kind of neurons. This gives us an approximated dating of 15–20 million years for their inrush in the history of great apes. They are located in layer V of two areas: The first one and most important regarding the number of

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[38] Therefore they are also called *spindle cells*.

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 pointing out that (1) these neurons are computationally simpler than the pyramidal ones, and that (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. Recent work has discovered the presence of VENs in the human *disgranular dorsolateral prefrontal cortex*, concretely in the Brodmann area 9 (Fajardo *et al.* 2008) as it is showed in Figure 8.

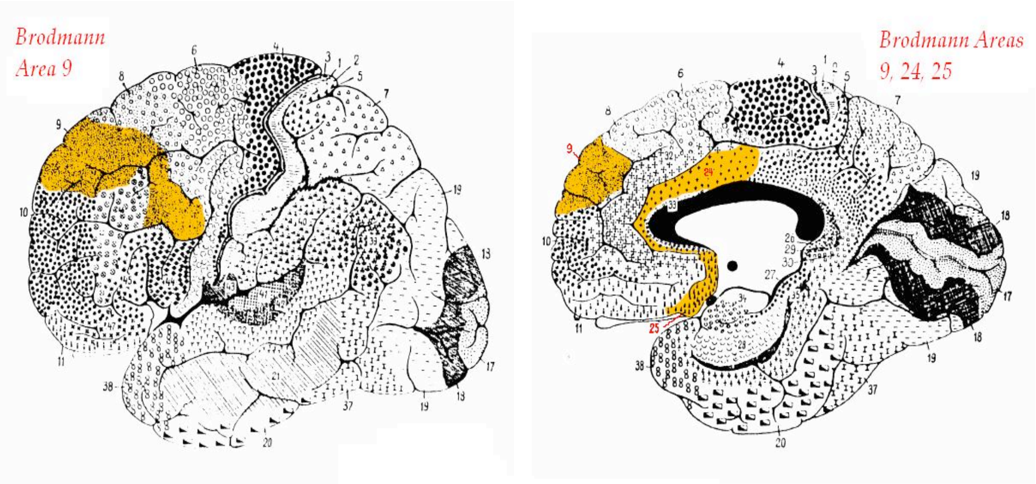

Figure 8: Human cerebral areas where von Economo neurons are located (picture modified from Wikimedia Commons)

Back to the comparative method, Nimchinsky *et al*. (1999) single out that this 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 mammals[39] (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 (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 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.

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

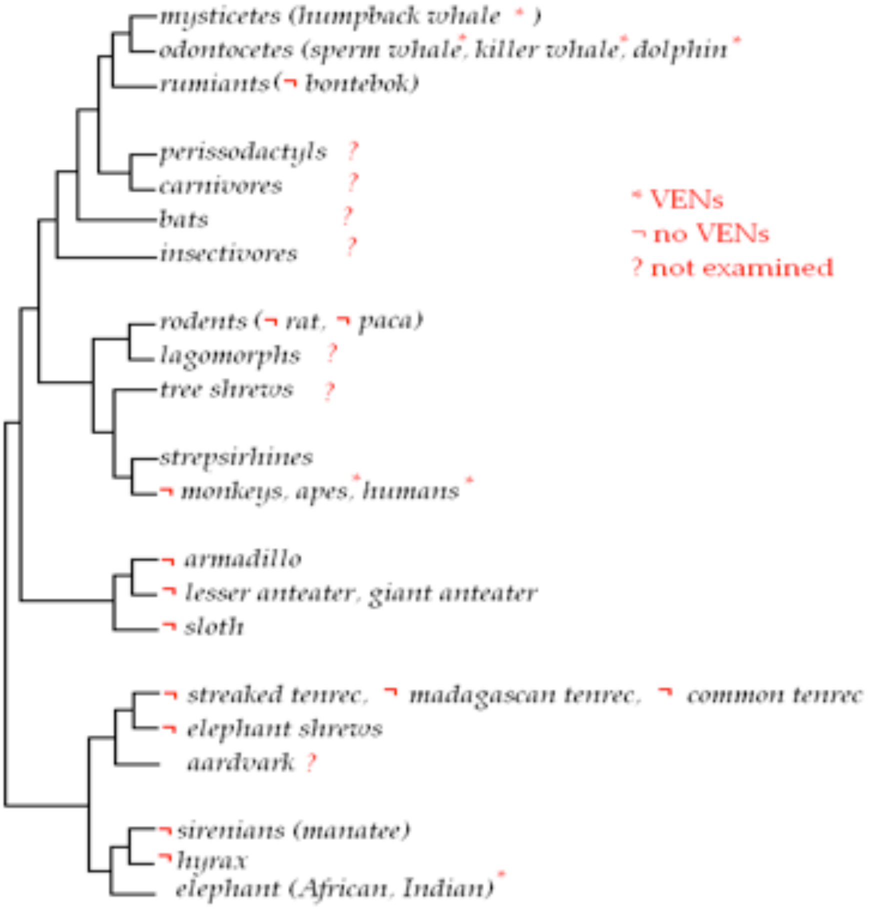

Figure 9: Phylogenetic tree with the species which either have or lack of VENs (adapted from Haakem et al. 2009)

In relation to the Neandertal man, it is interesting to note that it is possible to extract information 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 posited the presence of VENs as an archaic trait that has survived only in the extant species. 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. The distribution of such neurons in bonobos looks especially like that of humans, being the only two species which have clusters of VENs (Hof *et al*. 2000). Hence, it doesn't seem 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. Positing their absence in Neandertal brains would be counter-intuitive, if we take into account the current data referring the five great apes.

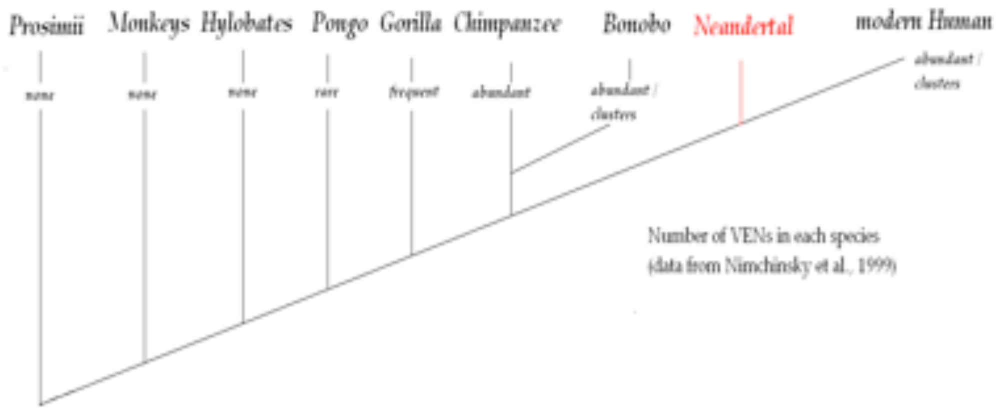

Figure 10: Phylogenetic cladogram and the distribution of VENs in primates

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 long-distance projections, but their exact connections still remain 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 8: 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 (in the area 24) indicates they have a relevant role in activities related to these areas. To the most basic ones, like breathing or cardiac rhythm, others should be added, which are actually related to emotions and vocalizations. 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 evolution[40] and, moreover, that it would participate in intuition or in pathologic cases like autism.[41] All this is consistent with what has been argued by Marino *et al*. (2007) about the cognitive abilities of cetaceans: 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 abilities, there stands out that cetaceans can recognize themselves in a mirror, can vocalize voluntarily and finally can make use of intuition. The two first abilities have also been positively proven in elephants, the other VENs mammal carriers.

All these lead me to think that the anterior cingular cortex is related to the production of vocalization with emotional content. If the presence of VENs gives us clues about some vocal abilities, diseases affecting them show us the pathological aspect that could affect vocalization: VENs are especially sensitive to fronto-temporal dementia (Seeley *et al*. 2006) and to Alzheimer (Nimchinsky *et al*. 1995). These diseases affect the three mentioned Brodman areas: 24, 25, and 9. Moreover, lesions in the ACC have been related to a kind of mutism.

If we assume that the brain of the Neandertal man had von Economo neurons at layer V in areas homologous 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* becomes very different from that according to which this hominin was unable even of producing sounds voluntarily or, 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 succinctly seen — 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 exclusive of modern human.

Next, I will analyze the question of FOXP2, 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 of a British family —

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[40] To some extent, such conclusions are based in the alleged postnatal emergence of VENs, which was thought to start up in the fourth month of postnatal life. However, Hayashi *et al*.'s (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 VENs appear continuously until the fourth year of live, whereas in chimps their proliferation downs rapidly in postnatal life.

[41] Besides 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 for intuition and (2) they are neurons that become dysfunctional in disorders in the autistic spectrum. According to this hypothesis, faulty VENs could partially be responsible for the lack of social abilities and this could lead to a lack of intuition.

under the pseudonym *KE* — which affected 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 announcing an analysis of FOXP2, a gene that codifies a protein belonging 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 amino-acids.[42] Such difference is reduced to two different amino-acids when the comparison is made with chimpanzees. Moreover, the authors argued 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 is the only primate who has a differentiated allele, with changes in two amino-acids. The date of the gene fixation in modern humans was calculated around 200k BP, coinciding more or less with the appearance of *H. sapiens* as species.

The family *KE* has a mutation of this gene[43] (Lai *et al*. 2001). Its effects have been directly related to their linguistic deficit by means of neuroimaging studies, which, once confronted to the results of the affected people with the non-affected people, show different patterns of activation in linguistic tasks: Affected individuals are less active in regions related with phonological processing (according to the authors this would explain the verbal dyspraxia) and in other sub-cortical areas like the basal ganglia.[44,45]

This gene was no more considered exclusive of *H. sapiens* when Krause *et al*. (2007) accomplished the difficult task of obtaining Neandertal DNA in good conditions[46] and manage to identify the gene *FOXP2* in the DNA of both Upper Paleolithic hominins. This fact changes radically the picture: If *H. neanderthalensis* had the same gene with the very same amino-acid substitutions than current

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[42] Genetic nomenclature can be a little bit confusing: (i) When talking about the gene in general, it is written FOXP2; (ii) when talking about the human variant of the gene (the allele), it is written *FOXP2*, and its protein is FOXP2; (iii) when talking about the variant of the mouse, it is written *FoxP2* and its protein is FOXP2. More information can be found in HUGO (http://www.genenames.org/guidelines.html#2.%20Gene%20symbols), the Guidelines for Human Gene Nomenclature.

[43] Specifically, a conversion G → A. Other patients who didn't belong to 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.

[44] As we will see, these areas are important according to Lieberman's hypothesis, which will be reviewed in section 4.5.

[45] A different kind of vocalization that has been linked to FOXP2 is that of 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: 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, a work that points out that pups could do that in stress conditions has been recently published (Groszer *et al*. 2008). Hence, it seems that Foxp2 is not essential for vocalizing ultrasounds (Fisher & Sharff 2009).

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

modern humans, it could have got the same benefits (and damage) humans have. More interesting, though, 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 opposite. 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 small size of the sample both Green *et al*. (2006) and Krause *et al*. (2007) counted with. Finally, a very recent publication shows results confirming the emergence of this mutation as ancestral in Neandertals, that is to say, as appearing before the split between modern humans and Neandertals (Burbano *et al*. 2010).

Trait	***H. neanderthalensis***	***H. sapiens***
FOXP2	√	√

Table 9: Gene FOXP2 in both hominins

The importance of this gene is not only due to the fact that it is a derived trait present today only in humans, but also due to its implications in motor operations aimed at vocalization. Thus, before they split off, both *H. neanderthalensis* and *H. sapiens* 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 any 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, Wassink *et al.* 2002), though very controversial (see Newbury *et al*. 2002), and schizophrenia (Levy *et al*. 2010, Sanjuan *et al*. 2005, 2006). I simply point out that the Neandertal man could have been a potential subject of such pathologies in case the supposed role the *FOXP2* gene plays therein is finally confirmed.

4.4. *Mirror Neurons and Motor Theories about Language Origins*

Mirror neurons have been detected in the brain of rhesus macaque *(Macaca mulatta*). 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 consists in grasping something, the action is called *transitive*. When it consists in a similar movement, though without grasping anything, the action is

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[47] I make this specification about the genus *Homo* due to the DNA proofs mentioned above about the mysterious hominid at Denisova cave (Krause *et al.* 2010). Reich *et al.* (2010, 2011) have recently analyzed nuclear DNA and mtDNA from the Denisovan. The results clearly show that Denisovans were a sister group split from Neandertals. Denisovans interbred with the new African incomers so that today some Melanesian populations still have Denisovan inheritance in their genomes. Though FOXP2 is not discussed in these works, the (expected) presence of the 'modern' allele has been confirmed. I thank Martin Kircher for confirming this piece of data. Anyway, the most recent common ancestor (either *H. heidelbergensis* or *H. antecessor*) of these hominins should also have the modern version of the gene.

called *intransitive*. These neurons have still not been detected in *H. sapiens* brains directly, though there is 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 helps 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 area F5, which seems to be the homologous one to 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 into 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 by happenstance that the motor control and the traditional linguistic areas (Wernicke and Broca's area) are located in the left hemisphere. This has been related to the lateralization of language and the difference between both hemispheres (Corballlis 1993).[48] Corballis has affirmed that, in comparison to other non-human primates, our hominin forebears were better 'pre-adapted' and had more intentional control on bodily movements than on intentional vocalizing (Corballis 2010: 27). In the same line of argument, he explains that gesture was *conventionalized*[49] in the first place and from this point "[i]n 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: 28). Corballis considers that this change was gradual, almost imperceptible. An explanation of this evolutionary process has been put forward in Gentilucci & Corballis (2006).[50] Nonetheless, in my view, this proposal still has several pitfalls. The authors rightly point out that the cortical control on speech is a fundamental element. However, their hypothesis relies on arguments that are not supported anymore by the last findings in evolutionary studies, as I have noted elsewhere (Barceló-Coblijn 2011). For example, the emergence of *bipedalism*, which would have freed the hands (Gentilucci & Corballis 2006: 951), has serious problems, since Lovejoy and colleagues (Lovejoy, Owen, Simpson *et al.* 2009, Lovejoy, Owen, Latimer *et al.* 2009, Lovejoy, Owen, Suwa *et al.* 2009) show that (1) *Ardipithecus ramidus* was biped, and (2) *knuckle walking* is a derived trait independently appeared in both

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[48] Lateralization has been confirmed in gorillas (Cantalupo & Hopkins 2001) and in chimps (Hopkins & Cantalupo, 2004; Hopkins *et al*. 2007).

[49] Notion borrowed from Burling (1999).

[50] See section 5, on the problems of dating the emergence of speech. I thank Michael Corballis for reminding me that Gentilucci & Corballis (2006) have already addressed the question of the gradual evolution of speech.

chimps and gorillas. Gentilucci & Corballis (2006: 953) assume Liberman *et al.*'s (1967) theory of speech as gesture, considered quite controversial by many scholars. The authors then assume that "the basic unit of speech, known as phoneme, does not exist as a discrete unit in the acoustic signal". I prefer the separation of phonemes as abstract psychological entities belonging to phonology, and phones or sounds as the units of speech. Some emphasis is also put on signed languages. However we must not forget that these languages are the exception rather than the rule. In fact, today there are many. Most of them emerge due to pathological reasons and it is not until recently in our history that important communities of deaf people have come together and made possible the emergence of such languages. Altogether there seems to be indications of the plasticity of the human brain which makes possible the externalization of language through other non-oral channels. Along Hockett's lines, if our evolutionary history had been different and we had evolved a prehensile tail like some American monkeys, we surely would have add this 'fifth limb' to our external expressions, as well as in signed languages too (Hockett 1964: 144). Another argument is the exclusivity of FOXP2 gene, nowadays problematic due to the aforementioned reasons. Finally, Gentilucci & Corballis (2006: 954) say that "[t]he course of events in the evolution of language may be paralleled by those in the development of language in children". I really think that today we have to resist arguments based on the idea that "ontogeny recapitulates phylogeny", an apparently superseded debate (Gomila 2010). The connections between hands and mouth are there. This is something clear, at least at the neurological level. However, what it is not so clear is why one should posit a linguistic stadium were signs are fully dominant, when mammals' main communication channel is oral. Indeed primates stand out in oral signs along with other gestures. Perhaps we should not posit stages without sounds or without signs, but stages where both externalization possibilities are present, complementing each other. Indeed multimodal approaches like this are all but new (Hockett 1978: 295–300).

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 that they do so only 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, as far as cognition and available data are concerned. 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). A recent work shows that this was also the case between *H. sapiens* and Denisovans — an Asiatic hominid branch separated from Neandertals after leaving Africa (Reich *et al*. 2010, 2011).

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. Altogether it seems, rather on the contrary, that 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. It is possible to conceive differences between Neandertal cognition and *H. sapiens* cognition and, in fact, there has always been a trend defending such differences, which would have tipped the balance in favor of the supremacy of the African hominin (*H. sapiens)* over the European one (*H. neanderthalensis*). The Neandertal man found a comfortable enough ecological niche in Europe and near Asia 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: (i) a lack of stimuli or pressures that favor variation or (ii) an incapability to develop more complex technology and material culture. This issue is currently debated. I just point out that 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, 2009, 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.[51]

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 it is difficult to fit the Neandertal man in the current Corballis' theory, as it is right now, without substantial modifications, we can perfectly concede some room for variation in the configuration of the neuronal cables and, especially, 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.

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[51] Corballis recalls that most archaeologists, though, say that the sophistication of material culture in *H. sapiens* vastly exceeded that of the Neandertals from about 75.000 years ago. I agree with that. The point is that the quantity and quality of Neandertal material culture (MC) is quite different in both quality and quantity from the Oldowan MC or even the Acheulean MC. New evidences of quite modern behavior are appearing day by day, so that it is difficult to speak about species-specific limitations: It seems that Neandertals purposely collected feathers (Peresani *et al*. 2011), had beds and hearths (Cabanes *et al*. 2010) and knew about pigments (d'Errico *et al*. 2010). Of course, one can easily detect qualitative differences between objects arguably left by Neandertals and objects made by Sapiens.

Trait	***H. neanderthalensis***	***H. sapiens***
Mirror neurons	*	√

Table 10: Mirror neurons probably were present in the Neandertal man's brain

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 subcortical structures, like the basal ganglia, to the already superseded theory on both the areas of Wernicke and Broca.[52] Lieberman reminds us that an aphasia of Broca — an argument used by Corballis — is never only cortical, 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 *et al.*'s (2009) experiments show modifycations in the neurons that make use of dopamine as a neurotransmitter, and in the basal ganglia.[53] 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. This hominin has also the 'human' version of the gene. Hence, it is expected that its expression would also have affected somehow the basal ganglia of Neandertals in the same way 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: 802). He does not offer instead 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 with each other. Nevertheless, until these theories do not abandon the strategy of placing both their starting and finishing points 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 calling into question the alleged specificity of the trait in question (be it mirror neurons or basal ganglia). In my view, none of these theories invalidate the inclusion of

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[52] 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 ago to a net of areas integrated in one only system. 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 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.

[53] 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).

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 on 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 progressive. Data regarding the vocal tract and the neuronal apparatus that supports it are more conclusive: During the process of *hominization*, there has been a continuous stream of changes and exaptations that has flowed into the 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 the capability to emit vocalizations which have previously been analyzed by a system which is able to put elements in order, to sequence and to categorize sounds, then we must be cautious, because other species (not only primates) have some of these aspects as their own, and it seems that such species have acquired some of these 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 Figure 3). To date, a gradual process like this is very difficult.

The gradual perspective is coherent with data that have been found thanks to the comparative method, in such a way that they indicate a previous stadium of phylogenetic unity (e.g., the air sacs) or of evolutionary convergence (e.g., von Economo neurons). In this sense I coincide with Fitch, Lieberman or Corballis, though my approach tries to integrate what we know from different fields of study. Coincidences between authors in this respect are few indeed: Lieberman (2007) shows his disagreement with Corballis' (2002b) datations, who places 50k BP the emergence not only of modern speech, but also of the grammatical capacity all humans around the world share. I agree with Lieberman (2007) that this seems to be impossible: the datation of humans' arrival to Australia — as confirmed, by example, 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), suggest that, as it has been argued in Barceló-Coblijn (in press), we must move back both capabilities to a temporal point previous to the out of Africa. Dates about the 'emergence of vocalization' used by Corballis have changed in time: 50k BP (Corballis 2002b), qualified by Lieberman as "virtually impossible" (Lieberman 2007: 559); 200k — 170k[54] 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). These datations would not be especially relevant but for two reasons: (1) If

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[54] In the abstract it says 170.100, probably a misprint.

we talk about a gradual process of biological evolution, how can limits be established? It is not clear why we should select a datation, when the trait evolves so slowly and, hence, with very diffused limits; (2) part of Corballis' arguments are based on the FOXP2 gene. For this gene, the author sees as more feasible the dating Coop *et al*. (2008) offered, around 42k BP (the authors argued contamination in Enard *et al*.'s 2002 work). This seems unlikely, as we have already seen when talking about FOXP2. The last results (Burbano *et al*. 2010, Green *et al*. 2010, Reich *et al*. 2011) point to two important facts: (i) 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*; (ii) the hybridization with Neandertals and Denisovans has been proven, though, as above mentioned, to be of the *introgressive* type. So, it has been proven the hypothesis that Neandertal would have not obtained the derived *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 11, show us a richer picture of 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.

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

Table 11: Summary of traits related to speech

Looking at Table 11, 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 arguments enough to take them into account. 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 to 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 the one I have offered it is possible to 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 only in *H. sapiens*.

Noam Chomsky has defended for more than forty years the idea that syntax has a (very powerful) structural component, which allows us to build linguistic structures virtually limitless or only limited by external components — 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. For example, an interesting approach is the one developed by Camps & Uriagereka (2006). They try to test the presence of syntactical capabilities from non-linguistic activities which could follow a recursive patterning, like knotting. Making knots, but also other activities like basket weaving, suggests the participation of a mind ready to sequence complex patterns like these (Barceló-Coblijn & Gomila, in press).

The goal of this work was to go deeply into 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. Future research will confirm some aspects that remain doubtful and perhaps also single out new ones, regarding both *H. neanderthalensis* and *H. sapiens*, in order to shed some light onto the biological history of these two hominins, and figure out which cognitive differences — if any — separate and distinguish them.

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