On the Relationship between the Air Sacs Loss in the Genus *Homo* and Duality of Patterning

Lluís Barceló-Coblijn [†]
lluis.barcelo@uib.cat

ABSTRACT

In a series of works, different models have shed light on the acoustic properties of *air sacs*, an organ located in the laryngeal region that is present in all great apes with the exception of humans. These works have shown how the loss of air sacs expands the number of possible digits but not the amount of signals per se. The number of signals in human language increased when the codifying property known as *duality of patterning* became characteristic of the codifying system, allowing digits to be combined in order for new signals to be codified. A direct relationship between air sacs and duality is presently being plotted, integrating linguistic theory and data from computational models into an evolutionary and developmental perspective of the evolution of modern speech.

Keywords: air sacs, duality of patterning, codifying system, combinatorial space, genus *Homo*

1. Introduction: air sacs and the genus *Homo*

Great apes in general could be argued to be similar in certain areas. Not just at the genomic level, but also regarding general morphology– for example, those traits that separate apes from monkeys – and even in some aspects of their behaviour. Nonetheless, there are some striking differences that provide interesting clues to divergent evolution, separating humans from the rest of great apes. Speech is one of these salient features. Speech is based on a highly specific vocal tract shape and a particular neuronal configuration (Ackermann, Hage & Ziegler, 2014). Thorough observation of the anatomy of great apes has verified one of the remarkable factors that make our vocal tract different

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[†] University of the Balearic Islands, Spain.

from theirs: the fact that modern humans lack air sacs, an organ located in the centre of the larynx (connected to the hyoid bone in other great apes).

All great apes with the exception of humans have air sacs and can use them in their vocalizations. It is intriguing, that such an evident physical trait as laryngeal air sacs has not attracted more attention in evolutionary studies of linguistics. It was Fitch, who first demanded more attention for this apomorphy of the genus *Homo* (Fitch 2000; Hauser & Fitch, 2003). Thus, a frequent question is, when – in the lineage *Homo* – did these laryngeal air sacs disappear? Part of the answer has been related to the shape of the hyoid bone: it clearly shows the presence or absence of air sacs in great apes. According to what we have seen until now, the absence of air sacs in the genus *Homo* goes back at least to *H. erectus* (Capasso et al., 2008).

However, it is still uncertain whether *H. habilis* already lacked that organ, because no hyoid bone of this species has been found. What we know for sure is that the species *H. sapiens*, *H. neanderthalensis* and *H. heidelbergensis* share a "modern" hyoid bone (with some differences in comparison to *H. erectus'* hyoid bone), in the sense that there was no orifice to connect the air sacs. Some authors consider *H. heidelbergensis* as simply an archaic state of *H. neanderthalensis* and hence these two species could be considered as a single species (Stringer, 2012; Cela-Conde & Ayala, 2001). If this theory is finally accepted, then only two species - and not three - would be confirmed to have a derived hyoid bone. The Denisovan hominin could also be included, given its close relationship with *H. neanderthalesis* (Reich et al., 2010).

We do not know whether these sacs appeared before or after the emergence of the genus *Homo* or even the emergence of our own species. According to Ann MacLarnon,

> One possibility is that this occurred when the human thorax altered from the funnel-shape of australopithecines, to the barrel-shape of *Homo erectus*, as, in apes, air sacs extend into the thorax. It therefore quite probably occurred prior to the evolution of human speech-breathing control, and it may also have been a necessary prerequisite stage. (MacLarnon, 2011, p. 233)

Thus, it seems that the key lies in the use of the comparative method and the application of the principle of parsimony: many mammals have laryngeal air sacs; among the most representative and closely related to us, we find most primates, but also cetaceans.

Regarding cetaceans, Reidenberg & Laitman (2008) have made a physiological study where research was undertaken into the air sacs of two species: odontocets (for example, dolphins) and misticets (for example, whales). The former have three kinds of sacs (nasal, parapharyngeal and laryngeal) while the latter show only a single laryngeal sac (considered homologous to the one present in artiodactyls, such as the reindeer or the takin from the Eastern Himalayas). Nevertheless, the function of air sacs seems to be different in odotocets, in comparison to great apes. However, it is important for the present discussion to consider that the presence of that organ in misticets suggests how old this feature is in mammals. Of course, the function they serve can vary during evolution (following Love 2007, it is worth noting that it is structures – along with their activities – that *evolve*, but not functions).

Recent works have explored the acoustic characteristics of air sacs and have discovered a special influence of the sound produced by the air sacs on the sound generated by the vocal folds (de Boer, 2008; Riede et al., 2009). The results of these works coincide regarding the effect on vocal sounds, whose formants are affected by the sound of the superimposed air sacs. A recent work on acoustic perception by de Boer (2012) has shown that humans have difficulties in discerning the type of vowel sound when there is air sac intervention, pointing to co-evolution of speech and hearing. De Boer considers that, given the benefits of a vocal tract without air sacs, which counts on a richer vocalic space, the human vocal tract has evolved so that communication has been enhanced:

> If it is assumed then that the experimental results are due to lower distinctiveness of the stimuli and that communication is more successful when one is able to produce more distinctive signals, it follows that having an air sac attached to the vocal tract is an impediment for successful communication through speech. (de Boer, 2012)

I would like to propose a further analysis that takes into account de Boer's considerations about the acoustic evolution of speech. This analysis focuses on signal design and the factors intervening in human signals. This approach singles out the role of *duality of patterning* – a property of the human codifying system – in the expansion of signals. It is also shown how the eventual loss of air sacs has affected the combinatorial space within which the codifying system (and hence the property of duality property) operates. Hence, to understand better the relationship between the loss of air sacs and signal expansion, duality of patterning must be taken into account. The second section is devoted to the explanation of certain significant notions of language as a codifying system and the consequences of increasing (1) the number of primitive meaningless digits or (2) the length of the resultant signals. I will then go to show how the human capacity for classifying linguistic signals is not only tied to the typical linguistic sounds but also to other types of external input. These observations lead me to the final section where I will make a reflection on the evolution of air sacs and signalling in mammals, drawing special attention to primates.

2. Acoustics, hearing and air sacs

De Boer (2008) has recently created an initial physical model of air sacs in order to study this laryngeal organ. The results suggest that this organ has a relevant effect on vocalization. De Boer's model takes its inspiration from the morphological characteristics of the howler monkey (*Aoulatta guariba*). The author compared both kinds of productions and obtained very similar results: Howler monkey vocalizations have peaks around 300, 750 and 1410 Hz, whereas the artificial model reaches 215, 725 and 1215 Hz. De Boer has observed that, when air sacs are added to the model, the formants rise, reaching higher values and new frequencies, constraining the ability to articulate new sounds. This could be the reason, the author argues, why air sacs were lost during the evolution of genus *Homo.* Notwithstanding, de Boer points out that the remaining functions attributed to this organ could be equally valid and, for the moment, he sees no reason to reject them (on this matter, see section four). Riede and colleagues (2008), in their turn, have created several models and their results point to an increase of the variability of the impedance of the vocal tract. Coinciding with de Boer, the results of Riede's team show that air sacs destabilize the sound source. The authors have recently created a progressive model to which new elements (the larynx, the bulla, the air sac, etc.) are added in order to compare the results of each "phase". The authors have taken into account currently available data on the Siamang (*Symphalangus syndactylus*, from the family *Hylobatidae*), who are known to fill the air sacs during their "boom" call. Riede and collaborators detected two acoustic effects produced by the air sacs: 1) air sacs increase the dynamic range of sound emission, but only at the higher and lower limits; 2) the vocal variability can be increased in different ways, some of them subject to non-linear and unstable phenomena.

It has been argued that the conception of co-evolution of vocal tract anatomy and hearing is possible (Barceló-Coblijn, 2011a, 2011b) – and certainly appealing for a more emboddied and (evo-)developmental approach to organic evolution. In other words, speech goes hand in hand with hearing, since, for a sound signal to be voluntarily emitted with a communicative intention, the sender has to be able to (1) recognize the signal, and (2) categorize it as a linguistic signal. De Boer, (2012) has proven that modern humans find it more difficult to perceive vowels properly if vowels are modified by the superimposed sound of air sacs. The participants recognized them as linguistic sounds, but had problems to determine the identity of a pair of vowels (for instance, [I] was confused with [y], both native sounds in Dutch, the participants' language). Thus, data from both acoustics and perception studies suggest that, on the one hand, the presence of air sacs makes it somehow problematic for humans to perceive speech sounds adequately. On other hand, the data also suggest that for a human-like "speech system" it is better not to have attached air sacs to the laryngeal structure, in order to produce a wider range of speech sounds. How do these findings relate to the modern speech capability of humans?

In what follows, I will argue, following de Boer and Riede and collaborators, that the loss of air sacs was crucial for the evolution of modern speech in its current form and that the disappearance of this organ has affected the inventory of primitive sounds. In addition, I will connect this acoustic aspect with a second one, directly related to the recently evolved codifying ability of humans. Importantly, this ability is strongly based on the property of duality of patterning. Finally, I will highlight another important point, more psychological in nature, for the creation of signals: the capability of perceiving different kinds of input – not just the typical linguistic sounds – that can nevertheless be categorized as linguistic signals.

3. On meaningless digits, duality and codifying systems

The linguistic signal has classically been identified as an arranged string of sounds. However, today we know that it can also be made up of bodily signs, as in sign languages. Language can be envisaged as both a thought system and a communication system – and, contrary to what some scholars think, both are not mutually exclusive. Regarding the latter aspect, there is a wide agreement that humans are able to codify linguistic units made up of primitive sound/sign elements. The identification of this codification process goes back to Martinet (1960) and Hockett (1958, 1960). It was Hockett who identified the linguistic property of *duality of patterning* or simply "duality". As such, duality allows the codifying system to combine a discrete set of primitives into strings of elements (these can be for example sounds, movements or lights). Each string codifies a particular *meaningful unit*. Hockett called the primitive elements "cenemes" and the final codified and externalizable units, "pleremes". According to Hockett, in human language morphemes (and not words) are the most equivalent to pleremes, because they are discrete units codifying a meaningful unit. Morphemes have a phonological "envelope" that facilitates their externalization. The influence of Shanon's Information Theory in Hockett's conception of duality is deep (Barceló-Coblijn, 2012; Fortuny, 2010), so that a degree of abstract thought is required to understand his vision of language as communication system.

To understand better the relationship between the loss of air sacs and signal expansion, duality must be taken into account. For example, in Table 1 we find a description of a possible code. It is very simple: it has only two primitive meaningless elements (*cenemes*), namely A and B. It is thus a quite simple binary code. The codifying system must be able to codify meaningful units, in order to be externalized. Once codified, the system will then have of an inventory of *meaningful signals* (or *pleremes*) at its disposal – it is important not to confuse meaningful "units" with meaningful "signals"; the former will be codified into the latter. For example, the meaningful unit denoting "plurality" is codified, in general, into the meaningful signal "-s" in Catalan language (e.g., *llop* > *llops,* "wolf > wolves"), whereas in Italian language it is used, in general, a vowel (e.g., *lupo* > *lupi*, "wolf > wolves"). Hence, both Catalan and Italian have the same meaningful unit, but different signals. Hockett did not offer any label for the meaningful units. Some scholars call them *lexical items* (Barceló-Coblijn, 2012; Boeckx, 2008; Ott, 2009). In Table 1, code-words/pleremes may have up to 4 possible lengths (from 1 to 4 digits). As we have seen, the reduced inventory of cenemes forces the codifying system to reuse these primitive digits once and again.

2-digits code (cenemes: A, B)				
Length of the code-word		Code-words (pleremes, meaningful units)	N	Set
1 digit-long	2^1	A, B	2	α
2 digits-long	2^2	AA, BB, AB, BA	4	β
3 digits-long	2^3	AAA AAB BAB ABA BBB BBA ABB BAA	8	γ
4 digits-long	2^4	AAAA BBBB ABBB BAAA AAAB BBBA BBAA AABB AABA BBAB BAAB ABBA ABAA BABB BABA ABAB	16	δ

Table 1: A binary code and several possible code-word lengths. Sets refer to all possible combinations determined by the length and the number of digits. The number of digits is always 2 and the length of the code-words are the exponents.

Interestingly, the signal expansion of a system depends on the previous expansion of two sets: the set of *meaningful units* and the set of *meaningless digits*. The latter will be the combinable material for the codification of the meaningful units, so that new signals can be created.

It is crucial to know the kind of system and the constraints it imposes on the length of the signal. Some codes allow only one type of length (for instance, in Table 1, only α or only β). Importantly for the discussion of language evolution however, other codes could allow different signal lengths (for instance, α *and* β, or α *and* β *and* γ). As we see, the maximal Combinatorial Space (CS) of the code is related to the sum of the number of digits elevated to the length of the code-word:

(1)
Code $C_k = \alpha + \beta = 2^1 + 2^2 = 6$ possible code-words

Code $C_i = \beta + \gamma = 2^2 + 2^3 = 12$ possible code-words

When a codifying system has duality, it usually codifies some signals from among those that are possible. However, in animal systems, like *H. sapiens'* duality rarely makes use of all possible combinations, exhausting them. In the case of human languages, this is certainly the case (many possible combinations do not come up as morphemes). This fact increases *redundancy*, a property that enhances the probabilities that a message will be decoded, and hence communication will be successful. Nevertheless, this fact makes the code more prone to changes (an aspect leading to the evolution of multiple languages). Imagine that DNA is a conventional code. It has 4 digits (G, C, U, A), but the code-words can only be 3-digits-long: thus, the combinatorial space is $4^3 = 64$ possible code-words. It has been proven that all possibilities exist and represent different codons. Thus, this is a robust code that does not allow much manoeuvrability.

So far, we have seen how a codifying system with the property of duality operates. Other systems could behave differently, for example, attributing one different ceneme/digit to each meaningful unit. For small codes, this is no problem. However, in order for the code to be expanded, it will eventually need more and more *memory*.

As I will explain, the loss of air sacs – along with other evolutionary changes – has made the expansion of the set of *cenemes*, i.e. the meaningless digits possible in humans (also called the *alphabet* of the code). However, the disappearance of air sacs did not directly affect the set of public signals, since this depends on the codifying characteristics of the system (see next section). Interestingly, we will see that the very same morphological change has happened in many species, though it has not always been accompanied by an increase in cenemes. Before approaching evolutionary explanations, I will summarize the most important factors intervening in human signal design.

4. Factors in the composition of human signals

Human language allows different kinds of combinations, thus providing different lengths in the code-words (the morphemes). But this fact, although affected by the number of digits (say, phonemes or signs), does not directly affect the final number of signals. The codifying system is in charge of this task.

When air sacs disappeared, the possible number of sounds was altered, progressively increasing because, in the genus *Homo*, it was also followed by a change in the vocal tract (Boë et al., 2002; Boë et al., 2004; Barceló-Coblijn, 2011a). However, the number of phonemes – psychological entities – also had to increase. Nonetheless, this aspect was dependent upon cognitive changes, not just physiological ones. However, the number of public signals was still dependent upon the codifying system.

Some animals have the capacity of producing more oral sounds than they actually do (for example, the nightingale can produce around 1000 notes, but this bird usually sings around 200 songs; see Hurford, 2011). It is probably ecological factors, among others, that do not push them to exhaust the possibilities of their oral capacity.

If our ancestors, instead of developing a system that allows combination of several code-word lengths, had evolved towards a rigid system based on a single, though larger code-word length, then the number of signals would have probably increased. However, the CS would still be much more reduced and dependent on memory resources. Let us see an example, using the information from Table 1:

If a Code C_1 (with a CS= $2^2 = 4$) increases by one the number of digits (cenemes), but the length remains untouched, then CS= $3^2 = 9$ possible code-words. However, if Code C_1 evolves to Code C_2 (with a CS= $\beta + \gamma = 2^2 + 2^3 = 12$ possible code-words) – i.e., allowing two different lengths –, the CS of possible code-words is larger than in C_1. Of course, a combination of both more digits and lengths would increase the number of code-words enormously, as is the current case of human languages.

Additionally, humans can combine pleremes, a further step in the evolution of language (the so-called *compounds* like "fire-fly"). In this case, it is *productivity* (Hockett, 1961) – somehow similar to *recursion* (Hauser, Chomsky, & Fitch, 2002) – that has been argued to be involved in compounding (Rosselló, 2006; Barceló-Coblijn, 2012a).

Human public linguistic minimal signals, the morphemes, seem to be affected by several different factors: Firstly, the set of basic meaningless digits (or cenemes), which is determined by a complex relationship between the mind and body. For example, in oral languages, the morphology of the vocal tract has to go hand in hand with a proper mental representation and categorization of the sounds – hence intervening both speech- and hearing-related brain areas (e.g. Stowe, Haverkort, & Zwarts, 2005; Ackermann, Hage, & Ziegler, 2014). For this reason, a belch is not categorized as linguistic sound. Even some possible but quite unusual speech sounds such as the clicks of Bantu languages, would not be categorized in the "linguistic" category the first time, if the adult hearer has no previous experience with them (see next section on phonology). As we have seen, it is this first factor that is affected by the loss of air sacs in the genus *Homo*, in a complex series of evolutionary changes affecting both the physical morphology of the vocal tract and neural connectivity and activity.

Secondly, the length of the code-word (in the case of morphemes) is affected by Zipf's statistical law (Zipf, 1936), which states that the length of a word is inversely proportional to its rank in a frequency table. Note that, in this case, "words" are the object, not "morphemes". In English (especially with words of Anglo-Saxon origin) it is easy to find a 1:1 relationship between words and morphemes; in many cases one morpheme equals one word (therefore many people believe that "duality creates words"). However, this 1:1 equivalence is certainly more problematic in Romance languages, for example, where mono-morphemic words are much less common. As noted above, when a word is made up of more than one morpheme, an additional mechanism has intervened: *recursion* (as defined in Hauser, Chomsky, & Fitch, 2002; but see Barceló-Coblijn 2012a for some problems of their definitions).

Thirdly, the list of *meaningful units* is strongly connected to cognition. It is the brain/mind that cognizes the list of meanings. In human languages it has been proposed that there is a Conceptual-Intentional module that is responsible for the creation of meaningful units (Chomsky, 1995, 2000). In the field of philosophy of language there is an even stronger thesis, according to which human thought cannot be separated from syntax, so that thoughts and meanings are directly affected and structured by syntax (Hinzen, 2006, 2011; Gomila, 2011).

And finally, there is the intervention of the codifying system. If it has the property of duality, it has the possibility of combining digits in many different ways. Thus, a code with duality makes available a more creative and structurally different set of signals, than a simpler code that can make use of repetition only (for example a code with a single digit ß, where all signals are the same but just a little bit longer: ß, ßß, ßßß, etc.). Importantly, a code with duality needs a smaller channel capacity (Shannon, 1948; Shannon & Weaver, 1949), and in psychological terms, there is an optimization of memory resources. Another side-effect of this kind of codes is an increase of redundancy, optimizing the message deciphering (Hockett, 1961, 1987).

Up to here, we have seen some important factors affecting the design of human linguistic signals and how they interrelate to each other. Most of these factors are not related *per se* to human cognition and, although the psychological nature of phonemes has been mentioned while describing the first factor, I would like to go more deeply into this latter question, stressing a really important aspect of human phonology that linguists have become aware of recently.

4.1 Another factor in linguistic signals

There is an important aspect that is directly related to digits: the cognitive device that interprets and categorizes them as linguistic digits or cenemes. In the previous section, it has been noted that most languages make use of sounds, which are categorized as phonemes by human cognition. However, the presence of sign languages highlights an important aspect: human "phonology" – traditionally related to sounds (from Greek, *phonos* "sound, voice" and *logos* "word, speech, subject of discussion") – also processes signs, or even lights. There also exist the so-called whistle-languages, like the Gomerian Spanish whistle language (GSWL) (Classe, 1957). It has been proven that whistlers of GSWL do activate the areas of the brain normally associated with spoken-language function (Carreiras et al., 2005). Hence, "phonology" is in fact a human capacity able to process different kinds of inputs as possible linguistic cenemes. It is for this reason that it has been observed that phonology is probably *substance-free* (Maihlot & Reiss, 2007). Humans would seem to have developed a kind of *signal*-logy capable of processing and classifying signs, sounds, or even lights into linguistic categories. This fact could somehow weaken the view that the human vocal tract evolved "for" communication, given that hominins could have made use of other kinds of signs, and not just the typical linguistic sounds.

5. An evolutionary reflection about the loss of air sacs and communication

In the previous section I have pointed out the apparent substance-free condition of phonology as a possible counter-argument to the view of vocal-tract evolution due to communicative pressure. Evolutionary theory has long ago observed that there are at least four factors in organic evolution: mutation, genetic drift, migration and natural selection. We should add other factors like introgressive hybridization (Mallet, 2005, 2008) and phenotypic accommodation (West-Eberhard 2003, 2005). I think that research in the evolution of air sacs could be benefited by an increase of the number of intervening evolutionary factors. De Boer (2012) has observed that the increase and enhancement of the vocal system once air sacs disappeared, suggests that natural selection could have favoured individuals lacking air sacs. This observation, argues de Boer, would fit humans. From this point I would like to extend the analysis on the evolution of this organ. Without making any claims against the intervention of natural selection – which ultimately selects phenotypes, rather than changes at the genomic level – , it is possible to make this hypothesis compatible with an enriched theoretical approach taking into account additional factors to natural selection. The theoretical approach I put forward also aims to include more than one species, and eventually, all mammals.

Let us consider the work by Hewitt and colleagues (2002) on the presence or absence of air sacs, in which a broad descriptive study of this trait has been carried out. The authors offer four cladograms where four macro-families of primates (124 species altogether) are depicted. I have summarized this information in the following table:

Species	*n* of species	With air sacs	Without air sacs
Strepsirrhini	8	35	3
Cebids and callitrichids	25	10	15
Cercopithecoidea (macaques, papio and cercopithecini)	40	9	31
Colobines, Hominoidea:	11	8	3
Gibbons	9	6	3
Hominoids	5	4	1
Total	128	72	56

Table 2 : Laryngeal air sacs in primates, according to Hewitt et al. (2002).

Additionally, studies on both cetaceans and primates suggest that air sacs are a fairly common trait so that the most parsimonious conclusion is, that in great apes the lack of air sacs is a derived trait, and their presence an archaic trait. Given that, among great apes, air sacs are only absent in *H. sapiens* – pathological air sacs aside (Giovanniello et al., 1970) – such an evolutionary novelty can be considered an autapomorphy of our species. Regarding the rest of the extinct hominins of the genus *Homo* that eventually cohabited with *H. sapiens*, this feature is shared, at least, with *H. neanderthalensis* and *H. erectus*. Hence, we could talk of an apomorphy of the whole genus *Homo*, rather than an autapomorphy of a single species. However, to do that we still need to be sure about *H. habilis'* hyoid bone shape.

Reidenberg and Laitman (2008) have also considered the possibility that laryngeal air sacs in misticets could have an older origin in an archaic laryngeal ventricle, which would have moved away over time. Thus, we are dealing with an ancient feature in mammals, and therefore the observed functions are manifold:

Firstly, regarding cetaceans, Reidenberg and Laitman (2008) take into consideration (1) the increment of vocal resonance; (2) generating vocalizations underwater; (3) to prevent drowning; (4) to elongate the sound length; (5) to reuse the air once and again in vocalizations, given that they are mammals and have a limited access to air; (6) pumping air from the sacs to the lungs would allow them to use the same air volume again and again, making possible multiple vocalizations underwater; finally (7), the authors concede the possibility that, given that it is the energy of vibration which is transmitted through water, there could be a functional coincidence with the laryngeal ventricles of terrestrial mammals. Reidenberg and Laitman also point out a structural function (8), since the presence of the air sacs affects the general density of the head.

Secondly, regarding primates, the debate on the possible functions of air sacs still endures: (1) Negus (1949) argued that they were used for saving exhaled air; (2) Hewitt, MacLarnon and Jones (2002) in turn proposed a reduction of hyper-ventilation; (3) Fitch and Hauser (2003) believe that, on the one hand, primate air sacs can generate a new sound source; (4) on the other hand, these authors also proposed that this organ makes possible the production of stronger and longer lasting calls; (5) Hayama (1970, 1996) in turn, thinks that they are useful for softening pressure.

So, many morphological differences, in primates as well as in cetaceans, warn us that the functions of air sacs can vary from species to species. Probably, the first function they ever had will never be known. This multifactorial aspect of air sacs points to an extreme dependency relation between organ and (1) the environment and (2) the evolutionary history of each species. Altogether this suggests that function cannot be used as the first evolutionary argument. This seems also to affect the argument on communication. Many primates have lost their air sacs, and no improvement has been attested so far – at least, not in the same way as in humans. Moreover, field data have shown that there are species that could make use of air sacs to expand their signal repertoire. For example, Campbell’s monkeys, like many primates with air sacs, produce the “boom” call, which is basically the sound of air sacs (Ouattara et al., 2009). As it was mentioned in the introduction, this is also a possibility for Siamangs. On another front, McComb and Semple (2005) have found a positive correlation between the number of public signals and group size – although, when observed case by case, there are several exceptions. Importantly, these authors state that,

> It is important to note that the direction of causality cannot be inferred from correlational analyses, therefore it is not possible to say whether evolutionary increases in vocal repertoire sizes directly preceded or followed increases in levels of sociality (McComb & Semple, 2005, p. 383)

All this taken together makes me somewhat wary of focusing the evolutionary explanation on a single factor such as communication or natural selection, or size group. Instead, I think that a suitable explanation can embrace other additional factors too. For instance, species-specific mutations could have arisen independently in many mammals, bringing on the loss of air sacs. This is especially conceivable regarding the phylogenetic distance between primates, ungulates and cetaceans. Additionally, it would be interesting to take the developmental patterns of each species into account, recalling Evo-Devo ideas that go back to Alberch et al. (1979), Alberch (1989) and Oster & Alberch (1982). These proposals put forth the hypothesis that small variations could lead species in one direction or another, yielding different phenotypic morphologies in each case: for example, a group of primates that splits and evolves into several differentiated species could develop any of the attested air sacs morphologies, or even the lack of the trait. Different phenotypes are also possible even when two species have the very same genes (Pigliucci et al., 1996). Much more probable than a mutation is methylation. The loss of air sacs could also be due to the methylation of some of the genes involved in the development of this organ. As it is well known, gene methylation has an important effect in gene expression, since methylation can "deactivate" a gene. Methylation has also been referred as "reprogramming" (Mann & Bartolomei, 2002).

The variability in functions in addition to the great quantity of primates that have lost air sacs also suggests that – in some cases – such an evolutionary change could have neutral consequences in terms of survival. A subject that develops lacking air sacs still has the rest of the body and brain intact. It still can communicate, though in a rather different way. To the author's knowledge, there is no contrasted information about the reactions between coexisting species, which are close phylogenetically though different concerning the presence or absence of air sacs.

This altogether suggests that the loss of air sacs is a common change that may happen in mammals in general, and that could probably be rather neutral, given the number of species which have survived the loss of this trait. Once a species has evolved and has fixed the developmental path that yields the loss of air sacs, the intervention of natural selection and other ecological factors will certainly have their effect on the species. However, I would not eliminate but rather diminish the role of fitness and survival regarding the presence or absence of air sacs. Probably, as has been put forward, survival depends on many other factors that are not affected by the presence or absence of this organ. What would seem to be logical, as was pointed out in the introduction, is that there has been co-evolution of speech and hearing, and that when air sacs disappeared, auditory perception had to be ready to process the new available sounds.

Conclusions

In the present work I have reviewed issues on air sacs in relation to communication and signal design. I have noted that there is a direct relation between the loss of air sacs and the codifying system, and particularly with the property of duality. Whereas duality, as a property, has an effect on the combinability of digits and the structure of public signals, the absence of air sacs has had an incremental effect on the number of primitive elements with which a codifying system with duality can codify meaningful units. Finally, I have observed that human phonology may be considered substance-free, meaning that it deals with sounds (including whistles), signs or even lights. This point should be taken into account when theorizing about the evolution of air sacs in humans and their relation to communication. The presence and loss of air sacs are common traits in primates or in other species such as cetaceans or ungulates, suggesting that air sacs are an ancient feature in mammals. Finally, I have observed that nowadays, many different functions for this organ have been attested. Because air sacs have disappeared in many species, it is difficult to base the evolutionary explanation of such a loss only in functional terms. Therefore, I have included other factors also intervening in evolution, minimizing the role of natural selection, in favour of a multifactorial evolutionary explanation.

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