EXPLORING THE CONCEPT OF PHENOTYPIC ACCOMMODATION: THE CASE OF THE LOSS OF AIR SACS

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During human evolution our ancestors developed a new phenotype that excluded an organ present in all extant great apes: laryngeal air sacs. This change has been acknowledged as an important step towards modern human phonetics. However, to date there is little reflection about how to conceive such a drastic evolutionary change within the subtribe *Hominina*. Here we propose the theoretical integration of air sacs loss as a case of *phenotypic accommodation*, a notion that helps to understand how our ancestors managed to survive, accommodating and consolidating the phenotype without air sacs, paving the way for a new phonetic system.

1. Laryngeal air sacs and *Hominoidea*

Laryngeal air sacs is a primitive trait present in many mammals: cetaceans like dolphins and whales, some ungulates (e.g. takins, from the Hymalayas) and also in many primates. Hewitt et al. (2002) showed that, within 128 primate species, up to 72 still have this anatomical feature. Schön Ybarra (1995) attested up to four different kinds of laryngeal air sacs within primates: (1) lateral ventricular, (2) subhyoid, (3) infraglottal and (4) dorsal. The first one is present in all great apes with the exception of *H. sapiens*. Air sacs are present in juvenile apes, even in fetuses and neonates (Stark & Schneider 1960). Steele et al. (2013) used 3-D reconstructions and observed that air sacs in chimpanzees are lateral ventricular, extending in a position behind the clavicle bone.

1.2. Possible functions of air sacs

The relation of the vocal tract and air sacs and their potential functions is controversial, since their potential functions could be several and not all species use air sacs for the same functions: for saving exhaled air (Negus, 1949); for the

reduction of hyper-ventilation (Hewitt et al., 2002); for generating a new sound source and stronger and longer lasting calls (Fitch & Hauser, 2003). Lieberman (2011) notes that air sacs are probably related to vocalization since inspiring carbon dioxide-rich air is not as useful as controlling speech. Falk (1975) pointed out that the vertical movement of the hyoid bone also compresses the orifice of the laryngeal air sacs and hence, participating in the mechanics when air sacs are emptied out and filled up. De Boer (2008) and Riede et al. (2009) created several models showing the influence of the sound produced by air sacs on the sound produced by vocal folds, while experimental research shows that, when both kind of sounds become superimposed, modern humans have difficulties in order to distinguish vowels properly (de Boer, 2012). Although Harrison (1995) dismissed the idea that air sacs are not necessary for vocalizations, several scholars do not agree. Lieberman (2010: 333) recalls as well that another function of air sacs in gorillas is acting "like a resonating drum" when gorillas thump their chest. More recently, Perlman & Salmi (2017) analyzed the vocalizations of gorillas and suggest that this species could use them for male display.

1.3. Abrupt change and the view of complexity

During the evolution of the subtribe *Hominina*, laryngeal air sacs disappeared at some point. The key feature to discern the presence or absence of air sacs in the fossil record seems to be the morphology of hyoid bone. The australopithecine (*Au. afarensis*) hyoid bone found, by Alemseged et al. (2006) in Dikika (Ethiopia), shows a primitive morphology that would suggest the connection of air sacs to the respiratory system and, hence, to the whole apparatus in charge of speech. The shape of the Dikika hyoid shows a deep bulla, while the shape of the *H. sapiens* hyoid describes an arch, without that deep cavity on the body section. The deep bulla would be a result of the development of the individual, from the direct contact of the tissues of air sacs to the hyoid bone.

The next fossilized hyoid bone from the fossil record seemed to belong to a *H. erectus* (Capasso et al., 2008). That particular hyoid bone showed a modern morphology, i.e. there is no cavity or bulla shape to which air sacs could be in contact with. However, a second examination by Capasso et al. (2016) confirmed that that bone was "too thick and short to be the body of human hyoid". Finally, the neanderthal hyoid bone is quite similar to the *H. sapiens'* hyoid bone (Arensburg et al., 1989; Bar-Yosef et al., 1992).

Thus, at some temporary point of the early stages of genus *Homo* – somewhere between the *Australopithecus* and *H. erectus* clades–, an early hominin started making steps into modern speech. A plausible, falsifiable

hypothesis is that *H. habilis* could be that hominin. Suggestions about *H. habilis* capability for speech are not new at all (Tobias, 1987), but information about this hominin is still too scarce and contentious (Wood & Collard, 1999) and, hence, this hypothesis is, for the moment, still more grounded upon plausible ideas than upon solid data from the fossil record.

1.4. Modularity and complexity

The enigma of air sacs loss in our lineage needs an explanation integrating the fact that the tissue of an air sac is always in physical contact with other tissues: hard tissues (the hyoid bone) and soft tissues (muscles and ligaments). This fact establishes a direct relationship between them, since all tissues interact with each other, not only due to contact, but also through the movements of the body (e.g. movements of the laryngeal muscles when producing sounds or during deglutition; or while turning the head). In fact, this can be considered as a collection of interacting elements or, in other words, a complex system. In such systems, the deletion of some well-connected elements leads to a reorganization of the system.

The structure of organisms seem to present a modular building schema (Wagner, 1996; Schlosser & Wagner, 2004; Callebaut & Rasskin-Gutman, 2005). Heads have been analyzed as a complex system which integrates several modules and submodules, which include different sets of bones (more than 20), teeth (up to 32), a brain, sensory organs, muscles, ligaments, cartilages, veins, nerves, etc., showing altogether an evident modular organization (Lieberman, 2011: 8-12). Heads include the neck and all its hard and soft tissues. Inside the human neck two passages can be detected, one for the air and another for the food. Anatomical network analyses have revealed musculoskeletal modularity in primates (Esteve-Altava et al., 2015a; Esteve-Altava et al., 2015b; Powell et al., 2018).

In a recent network analysis of musculoskeletal organization, Powell et al. (2018) show that, in spite of having more musculoskeletal elements (up to 157), humans do not seem to be more complex than other great apes. These authors argue that "even major changes in function […] can occur without profound changes to the network organization and modularity of the whole system". Although Powell and collaborators include only direct musculoskeletal connections and not organs like air sacs, this reflection is still valid for the discussion on the evolution of air sacs: air sacs can disappear, as it has occurred in many taxa, without compromising the network organization, but affecting the function of the module. Following Powell et al. (2018), developmental plasticity

can facilitate the accommodation of functional and anatomical modifications without conditioning severely the network configuration.

Being it as it may, when an individual develops following a divergent and atypical developmental path, for example lacking (part of) an organ, the unexpected phenotype can provoke that other tissues of the system develop abnormally as well, due to the absence of physical opposition, and due to the "departure" –metaphorically speaking– from what was "planned" by the original, species-specific, body schema. Hence, soft tissues interact with hard tissues through physical contact. Lieberman recalls a good example of it in humans: an infant born lacking eyes will probably develop "tiny orbits with abnormally small upper faces because the eyeball normally pushes out the bones that form the orbital cavity walls" (2011: 53). Similarly, the air sacs loss had to have consequences for the surrounding tissues.

Other forces, like persistent muscular movements, if lasted through generations, could also exert an influence on the phenotypes, which could have been finally selected. Far from simply resorting to Lamarck's (1809) *Zoological Philosophy*, we advocate a hypothesis in which phenotypes, not mutations, are the selected ones (West-Eberhard, 2003). For example, recent analyses of dry skulls of both humans and chimpanzees suggest a link between the large number of mandibular movements of muscles involved in speech (much larger than those used in chewing) and the morphology of the mandibular space in relation to the tongue (Bermejo-Fenoll et al. 2019). In spite of the difficulty for showing a cause-effect relationship, Bermejo-Fenoll and colleagues could show that *H. sapiens*' ancestors followed an evolutionary trend which, progressively and increasingly, included more and more movements that today are related to modern speech, like for example lip smacking and oscillatory movements of the jaw (Ghanzafar et al., 2013; Ghanzafar et al., 2012; MacNeilage & Davis, 2005). Anyway, it seems out of question that, at some point between australopithecines and modern humans and –we suggest– after the disappearance of air sacs, the physical context of speech and the laryngeal structure changed, paving the way to new motor routines which could involve more (and perhaps new) movements that today are related to modern speech.

2. Air sacs loss as a case of phenotypic accommodation

West-Eberhard (2005a: 6547) recalls that "frequency of expression does not depend on the frequency of the inducer (mutation or environmental factor) alone". Thus, according to West-Eberhard's (2003, 2005b) proposal, evolutionary selection combines both natural and sexual or social selection, and hence, genes would be followers, not leaders in adaptive evolution. We think

this is a good theoretical framework for a change like the loss of air sacs. This is something that has not been yet approached and, thus, there are some possibilities open to inquiry. One possibility is that the first individuals lacking air sacs represented atypical phenotypes within their group of conspecifics. Hence, it is expectable that the disappearance of air sacs from the body schema altered, even if slightly, some developmental patterns during ontogeny, and thus yielding new, different phenotypes in adult individuals. Some available evidence from comparative studies do support such a view: works on the ontogeny of the descent of the hyolaryngeal complex and the root of the tongue takes place at about 3 months of age (Lieberman et al., 2001). By contrast, at 4 months of age the initial pouch that will become the air sac is already visible in chimps (Nishimura et al., 2007).

The observable fact is that this new phenotype somehow reached stabilization, and one of the reasons could be that it was not incompatible with survival. This can be interpreted as an indication (though still not confirmed evidence) of a fitness effect. According to West-Eberhard (2005a), if the new phenotype has a fitness effect, then selection occurs. Were this the case of air sacs loss, it could be conceived as a phenotype that has been consolidated, becoming the typical phenotype of current *H. sapiens*. Observed through this lens, thus, the air sacs loss could be classified a case of *phenotypic accommodation* (West-Eberhard, 2003; 2005b). Phenotypic accommodation takes place when an individual develops plastically, adapting the organism to new environmental inputs (here "environmental" refers to all levels in biology, from cells to ecological niches). If the new inputs persist and other conspecifics can develop the same adaptive phenotype as well, this new phenotype could become stabilized by, for example, new mutations promoting and reinforcing it.

Arguments supporting this hypothesis are, for example, that air sac loss is a consolidated phenotype in many primate species, some of them phylogenetically distant from one another (cf. Hewitt et al., 2002). Thus, it seems to be a recurrent homoplasy within the *Primates* order. Recurrent phenotypes with discontinuous phylogenetic distributions have been detected in many taxa (cf. West-Eberhard, 2003, for a highly detailed revision). Moreover, the existence of both phenotypes within *Primates* suggests ancestral developmental plasticity for producing both forms (West-Eberhard, 2005b: 6546). Were the air sacs loss phenotype dependent of a mutation (or methylation) only, it would be a mutation/methylation that has appeared many times and hence, less plausible. Thus, phenotypic plasticity seems to be a good candidate for the origins of air sac loss, given the fact that it can account for the repetition of homoplasies in different primates and in different stages of phylogeny. Moreover, phenotypic

accommodation could give time to this developmental variant for becoming stabilized within populations and species. The absence of air sacs would have led the possibility for some individuals to develop towards new phenotypes that were compatible with life (here we follow Pere Alberch's (1989) "logic of monsters" and assume the idea of a phenotypic space of biological possibilities). Let us remark that this hypothesis is conceived as a phenotypic possibility for some ancestors of *H. sapiens*, and not for all species that have evolved towards phenotypes lacking air sacs. The reason is that, usually, there is not a unique factor affecting the several environmental levels by which an organism is affected, and each species is affected by a different set of environmental factors (admittedly, partially coincidental with other species). The first individuals who developed like that, were at first unusual and atypical. However, some of their descendants managed to survive, consolidating (accommodating) a phenotype without air sacs, and thus paving the way for a new phonetic system.

Conclusion

Laryngeal air sacs is an ancestral trait in *Primates*, while its absence is a derived characteristic. Both possibilities exist in monkeys, lesser apes (*Hylobatidae*) and great apes (*Hominidae*). It is well-known that the descent of larynx does not guarantee vocalization (Fitch 2009). Similarly, the lack of air sacs does not guarantee neither the descent of larynx nor modern speech. But it was a necessary step for evolving towards what is known today as modern human speech. Nonetheless, both phenotypes are recurrent and it is puzzling how to integrate this into evolutionary theory. We propose that this could be a case of phenotypic plasticity and, more concretely, a case of phenotypic accommodation. This concept satisfies the recurrence of both phenotypes and the differences in ontogeny in juvenile chimps and humans. Finally, the concept of phenotypic accommodation solves the difficulty of linking this evolutionary change to mutation only, and gives the time a species needs until the new variant becomes stabilized.

Acknowledgements

References

Alberch, P. (1989). The logic of monsters: Evidence for internal constraint in development and evolution. *Geobios*, 22(2): 21-57.

Alemseged, Z., F. Spoor, W. H. Kimbel et al. (2006). A juvenile early hominin skeleton from Dikika, Ethiopia. *Nature,* 443:296–301.

Arensburg, B., Tillier, A-M., Vandermeersch, B., Duday, H., Schepartz, L.A. & R. Yoel. (1989). A Middle Palaeolithic human hyoidbone. *Nature* 338, 758–760.

Bar-Yosef, O., Vandermeersch, B., Arensburg, A., Belfer-Cohen, P., et al. (1992). The excavations in Kebara Cave, Mt. Carmel. *Current Anthropology*, 33: 497–550.

Bermejo-Fenoll, A., Panchón-Ruiz, A., Sánchez del Campo, F. (2019). *Homo sapiens*, chimpanzees and the enigma of language. *Frontiers in Neuroscience*, 13(558): 1-10.

de Boer B. (2012). Loss of air sacs improved hominin speech abilities. *Journal of Human Evolution*, 62(1):1-6.

de Boer, B. (2008). The Joy of Sacs. In A. Smith, K. Smith, & R. Ferrer i Cancho, (Eds.), *The Evolution of Language: Proceedings o the 7th international Conference (EVOLANG7)*, 415–416. Barcelona.

Callebaut, W., & Rasskin-Gutman, D. (2005). *Modularity. Understanding the development andEvolution of Natural Complex Systems*. Cambridge, MA: MIT Press.

Capasso, L., Michetti, E. & D'Anastasio, R. (2008). A *Homo erectus* hyoid bone: possible implications for the origin of the human capability for speech. *Collegium Antropologicum,* 32 (4): 1007-1011.

Capasso, L., D'Anastasio, R., Mancini, L., Tuniz, C. & Frayer, D. (2016). New evaluation of the Castel di Guido 'hyoid'. *Journal of Anthropological Science*, 20;94:231-5.

Esteve-Altava, B., Diogo, R., Smith, C., Boughner, J. C., & Rasskin-Gutman, D. (2015). Anatomical networks reveal the musculoskeletal modularity of the human head. *Scientific Reports*, 5(1): 1-6.

Esteve-Altava, B., Boughner, J. C., Diogo, R., Villmoare, B. A., & Rasskin-Gutman, D. (2015). Anatomical network analysis shows decoupling of modular lability and complexity in the evolution of the primate skull. *PLoS One*, 10(5): e0127653.

Falk, D. (1975). Comparative anatomy of the larynx in man and the chimpanzee: Implications for language in Neanderthal. *American Journal of Physical Anthropology*. 43:123–132.

Fitch W.T. and Hauser M.D. (2003) Unpacking "Honesty": Vertebrate Vocal Production and the Evolution of Acoustic Signals. In: *Acoustic Communication*. Springer Handbook of Auditory Research, vol 16. New York: Springer.

Fitch, W.T. (2009). Fossil cues to the evolution of speech. In: Botha, R., Knight, C. (Eds.), *The Cradle of Language*. Oxford University Press, Oxford, pp. 112–134.

Ghazanfar, A.A., Takahashi, D.Y., Mathur, N., Fitch, W.T., (2012). Cineradiography of monkey lip-smacking reveals putative precursors of speech dynamics. *Current Biology*, 22 (13), 1176–1182.

Ghazanfar, A.A., Morrill, R.J., Kayser, C., (2013). Monkeys are perceptually tuned to facial expressions that exhibit a theta-like speech rhythm. *Proceedings of the National Academy of Science,* 110 (5), 1959–1963.

Harrison, D. F. N. (1995) Detailed morphology. In *The anatomy and physiology of the mammalian larynx*. 48-184. Cambridge: Cambridge University Press.

Hewitt, G., MacLarnon, A. & K. E. Jones. (2002). The functions of laryngeal air sac in primates: Anew hypothesis. *Folia Primatologica*. 73:70–94.

Lamarck, J. B. (1809; 1914). *Zoological Philosophy*. London.

Lieberman, D.E. (2011). *The Evolution of the Human Head*. Cambridge, MA: Harvard University Press.

Lieberman, D.E., McCarthy, R.C., Hiiemae, K.M. & Palmer, J.B. (2001). Ontogeny of postnatal hyoid and larynx descent in humans. *Archives of Oral Biology*, 46: 117-128.

MacNeilage, P.F. & B.L., Davis. (2005). The frame/content theory of evolution of speech: a comparison with a gestural-origins alternative. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems*, 6 (2), 73–99.

Negus, V. E. (1949). *The comparative anatomy and physiology of the larynx*. 1st ed. W. Heinemann Medical Books.

Nishimura, T., A. Mikami, J. Suzuki et al. (2007). Development of the laryngeal air sac in chimpanzees. *International Journal of Primatology*. 28:483–492.

Perlman, M., & R. Salmi. (2017). Gorillas may use their laryngeal air sacs for whinny-type vocalizations and male display. *Journal of Language Evolution*, 2(2): 126–140,

Powell, V., Esteve-Altava, B., Molnar, J. et al. (2018) Primate modularity and evolution: first anatomical network analysis of primate head and neck musculoskeletal system. *Scientific Reports,* 8: 2341.

Riede T., Tokuda I.T., Munger J.B., Thomson S.L. (2008). Mammalian laryngseal air sacs add variability to the vocal tract impedance: physical and computational modeling. *Journal of the Acoustical Society of America*,124(1):634-47.

Schön Ybarra, M. (1995). A comparative approach to the nonhuman primate vocal tract: Implicationsfor sound production. In *Current Topics in Primate Vocal Communication*, E. Zimmerman and J. D. Newman, eds. New York: Plenum Press, 185–198.

Starck, D. & Schneider, R. (1960). Respirationsorgane. In H. Hofer, A. H. Schultz & D. Starck (Eds.), *Primatologia* (Vol. III (2), pp. 423–523). Basel: S. Karger.

Steele J, Clegg M, Martelli S. (2013). Comparative morphology of the hominin and African ape hyoid bone, a possible marker of the evolution of speech. *Human Biology*, 85(5):639-72.

Tobias, P.V. (1987). The brain of Homo habilis: A new level of organization in cerebral evolution. *Journal of Human Evolution*, 16(7–8): 741-761.

Schlosser, G., & Wagner, G. P. (Eds.). (2004). *Modularity in development and evolution*. University of Chicago Press.

Wagner, G. P. (1996). Homologues, Natural Kinds and the Evolution of Modularity. *American Zoologist*, 36:36-43.

West-Eberhard, M.J. (2005a). Developmental plasticity and the origin of species origin. *Proceedings of the National Academy of Science*, 102(1): 6543-6549.

West-Eberhard, M.J. (2005b). Phenotypic accommodation: adaptive innovation due to developmental plasticity. *Journal of experimental zoology. part B, (Mol Dev Evol)*, 15;304(6):610-8.

West-Eberhard, M.J. (2003). *Developmental Plasticity and Evolution*. New York: Oxford Univ. Press.

Wood, B. & M. Collard. (1999). The human genus. *Science*, 284, 65–71.