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Loss of air sacs improved hominin speech abilities

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ABSTRACT

In this paper, the acoustic-perceptual effects of air sacs are investigated. Using an adaptive hearing experiment, it is shown that air sacs reduce the perceptual effect of vowel-like articulations. Air sacs are a feature of the vocal tract of all great apes, except humans. Because the presence or absence of air sacs is correlated with the anatomy of the hyoid bone, a probable minimum and maximum date of the loss of air sacs can be estimated from fossil hyoid bones. *Australopithecus afarensis* still had air sacs about 3.3 Ma, while *Homo heidelbergensis*, some 600 000 years ago and *Homo neandethalensis* some 60 000 years ago, did no longer. The reduced distinctiveness of articulations produced with an air sac is in line with the hypothesis that air sacs were selected against because of the evolution of complex vocal communication. This relation between complex vocal communication and fossil evidence may help to get a firmer estimate of when speech first evolved.

Introduction

A major problem for students of the evolution of language is trying to date the emergence of complex vocal communication. There is very little fossil evidence for this, but air sacs have been proposed as a possible source of evidence (Fitch, 2000). Air sacs are large cavities connected to the vocal tract above the vocal folds and are present in all hominines, except humans (Hewitt et al., 2002). Given the prevalence of air sacs in apes, it is likely that the lack of air sacs in humans is a derived feature (Hewitt et al., 2002). A key question in human evolution is why air sacs disappeared, and whether selection for speech abilities played a role (Fitch, 2000; Fitch and Hauser, 2002; Hewitt et al., 2002; Nishimura et al., 2007). From fossil hyoid bones, a minimum and maximum date for the loss of air sacs can be deduced. *Australopithecus afarensis* still had air sacs at about 3.3 Ma (millions of years ago) (Alemseged et al., 2006), while *Homo heidelbergensis*, some 600 ka (thousands of years ago) (Martínez et al., 2008) and *Homo neandethalensis* some 60 ka ago (Arensburg et al., 1989), did not. Little is known about the selective pressures leading to the loss of air sacs. Here, the acoustic and perceptual effects of air sacs are studied to contribute to a more complete evolutionary scenario. Using an adaptive hearing experiment, it is shown that air sacs reduce the perceptual effect of vowel-like articulations. This finding is in line with the hypothesis that air sacs disappeared because of complex vocal communication.

Many mammals have air sacs (Frey et al., 2007) and at least five different anatomical configurations are recognized (Bartels, 1905; Frey et al., 2007). The air sacs found in apes are of the lateral ventricular type (Hewitt et al., 2002). These are relatively large, soft-walled cavities connected to the vocal tract through the lateral ventricles. They attach to the vocal tract just above the vocal folds and below the false vocal folds, passing between the thyroid cartilage and the hyoid bone (Fig. 1). In all hominines (chimpanzees, gorillas, bonobos, humans), the presence or absence of air sacs coincides with the presence or absence of the hyoid bulla (Kleinschmidt, 1938; Miller, 1941; Avril, 1963; Nishimura et al., 2007), a cup-shaped extension of the hyoid bone[1]. This may serve to keep open the connection between the vocal tract and the air sac.

There has been considerable debate about the exact function of air sacs. As they can become infected and form a serious health hazard (Lawson et al., 2006), they cannot be functionless, vestigial or accidental structures; there would be strong selective pressure against their presence. Most often, a direct acoustic function is assumed (Avril, 1963; Schön, 1971; Haimoff, 1983; Fitch and Hauser, 1995). However, experiments that surgically alter the air sacs of monkeys have given contradictory results (Gautier, 1971; Hilloowala and Lass, 1978), and an indirect role in vocalization, prevention of

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[1] It has been noted that orangutans do have air sacs, but do not have a hyoid bulla. However, the siamang (*Symphalangus syndactylus*) also has an air sac and a hyoid bulla. The absence of a hyoid bulla therefore appears to be a derived characteristic in orangutans, and may be related to their unusual submental anatomy (Brown and Ward, 1988).

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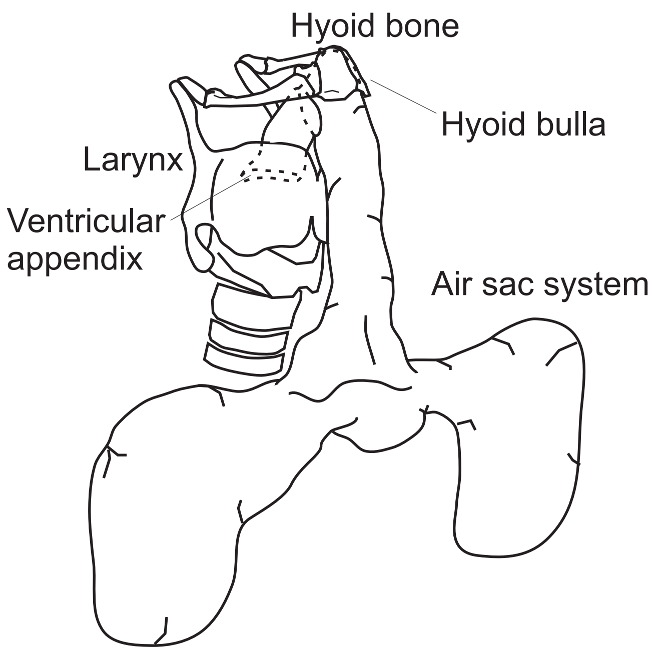

Figure 1. Chimpanzee air sac anatomy. Shown are the upper part of the trachea, the larynx (the cricoid and thyroid cartilages), the hyoid bone, the (right) ventricular appendix, and the connecting tube and cavity of the air sac.

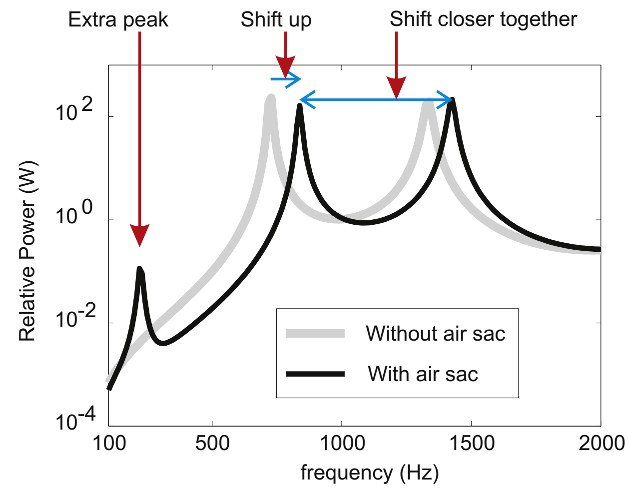

Figure 2. Acoustic effect of the air sac. Shown are the power spectra of the signal predicted for the articulation [a] without (gray line) and with (black line) an air sac. The most important changes are indicated with arrows: an extra peak near the resonance frequency of the air sac, and the shifting up and shifting closer together of the original resonances of the vocal tract without the air sac.

hyperventilation, has also been proposed (Hewitt et al., 2002). Lieberman (2011, 333), drawing a parallel with nasalized speech, has proposed that air sacs would make speech less clear. Most of the debate on the (acoustic) role of air sacs has been speculative, as physical models of the acoustics of air sacs were not available until very recently (Riede et al., 2008; de Boer, 2008, 2009). This paper investigates the acoustic and perceptual effect of air sacs on speech-like vocalizations using these new results.

To estimate the acoustic effects, it is assumed that the relevant vocalizations in the hominin lineage were, as in most apes, produced by vocal cord vibration, and that their perceptual quality was mainly determined by the resonance frequencies of the vocal tract. Theoretical and experimental analysis (Riede et al., 2008; de Boer, 2008, 2009) shows that when an air sac of ape-like size is connected as a side branch to an ape-like vocal tract, the original resonance pattern undergoes three main changes. First, a new resonance near the resonance frequency of the isolated air sac appears and acoustic energy at this frequency is radiated effectively through the air sac wall, thus increasing acoustic output at this frequency. Second, the original resonances of the vocal tract without the air sac are shifted up. Third, they are shifted closer together (Fig. 2). In addition, at higher frequencies, extra resonances and anti-resonances appear, which correspond to the higher resonances and anti-resonances of the air sac. As the lowest resonance of an ape-like air sac is below the lowest resonances of an ape-like vocal tract, these qualitative effects are independent of the articulation being produced (de Boer, 2009).

A consequence of these modifications is that the vocalization has more resonances per kilohertz, and contains more energy at low frequencies. This is known to create an impression of larger size (Fitch and Hauser, 2002), as well as allowing the sound to travel further in dense foliage (Gautier, 1971; Marten et al., 1977; Hombert, 2010). Both of these may serve adaptive functions.

But what is the effect of an air sac if it is attached to a vocal tract that is used for complex vocal communication? Would it diminish the perceptual effect of articulatory actions? As suggested by Lieberman (2011), nasalization seems to provide a parallel: it is also caused by attaching an acoustic side branch to the vocal tract (House and Stevens, 1956). It has been shown that the same articulatory actions have smaller perceptual effects when a vowel is nasalized (Wright, 1986). However, the acoustic effect of nasalization (House and Stevens, 1956; Dang et al., 1994) is different from that of an air sac, and therefore knowledge about the effect of nasalization is not directly applicable to air sacs. It is therefore necessary to do a perceptual experiment about the effect of air sacs.

Methods

To estimate the perceptual effects, and indirectly fitness due to communicative success, it needs to be understood how air sacs modify the relation between articulatory actions permitted by a given vocal tract anatomy, and the discriminability of the produced sounds. The effects of two deformations (Fig. 3) of a basic vocal tract were measured in a listening experiment with 22 human subjects (13 women, nine men, all native speakers of Dutch). The tract used approximates the human vocal tract shape for producing [a] (approximately the first vowel of English “father”) and consists of a narrow tube at the glottis followed by an equally long wide tube at the mouth. The first deformation approximates [ə] (the vowel of English “the”) and consists of a tube of uniform diameter. The second deformation approximates [y] (the vowel of French “tu”) and consists of a wide tube followed by an equally long narrow tube. These conditions ideally suit the purposes of this investigation as they represent simple articulatory actions (raising the tongue and closing the mouth from an open configuration) and can be implemented with two-tube models.

Generation of stimuli

Stimuli were generated on the basis of two sets of three Perspex models (all stimuli without noise are available as SOM). It was decided to use a physical model rather than a simulated computer model because existing speech synthesis models cannot deal satisfactorily with the three-dimensional nature of air sacs (the model worked out in de Boer (2009) only works at low frequencies and the model in Riede et al. (2008) approximates the air sac as a one-dimensional tube, rather than a three-dimensional cavity).