The acoustic role of supralaryngeal air sacs

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This paper presents a lumped element model of supralaryngeal air sacs of primates. It assumes that the air sac is connected to the vocal tract and plays a passive role in vocalizations (something which is most likely not the case for all vocalizations of all primates). It is shown that the most important factors influencing its acoustics (for the frequencies relevant in primate vocalizations) are the volume of air it contains and the mass of the walls. It is then shown that the spectrum of certain calls of *Alouatta guariba clamitans* can be closely approximated with this model when it is connected to a simple vocal tract model with dimensions that are realistic for the species involved. Finally, it is discussed how the model could be extended to become valid for higher frequencies.

1 Introduction

Supralaryngeal air sacs are an anatomical feature of many monkeys and apes [e. g. 2, for a recent overview]. They are inflatable sacs that are connected to the vocal tract *above* the larynx. There is considerable debate about the function of air sacs. Although their connection to the vocal tract would suggest a function in vocalization, other functions have also been proposed. These include the ability to rebreathe air [3], strengthening of the thoracic cage for locomotion using the arms [as discussed in 2] and a means to prevent hyperventilation during long vocalizations [2].

As for the role of air sacs in primate vocalizations, there are two things that they could do. They could change the resonance properties of the vocal tract, or they could change the impedance matching between the source of acoustic energy (vibration of the vocal cords or of analogous anatomical structures) and the surrounding air. In the case of *Cercopithecus neglectus*, it has been found that puncturing the air sac decreases the loudness and changes the timbre of vocalizations [4]. On the other hand, surgical removal of air sacs in rhesus macaques (*Macaca mulatta*) did not result in spectral change of vocalizations [5]. Another possible experiment to investigate the acoustic role of air sacs would be to have an ape or a monkey vocalize in a mixture of helium and oxygen (which has a different speed of sound than ordinary air) and see how the acoustic properties change. Such an experiment is difficult to execute, however, and to the best of our knowledge has not been done, yet.

Still, it would be interesting to better understand the potential role of air sacs in primate vocalization. Not just because air sacs are such a ubiquitous feature of primates, but also because humans do *not* have an air sac. Our closest evolutionary relatives, the great apes, all have air sacs, but we have apparently lost them. Furthermore, there is evidence from the anatomical features of fossil hyoid bones that *Austrolpithecus afarensis* [6] did have air sacs, while *Homo heidelbergenis* [7] and *Homo neanderthalensis* [8] did not. The question therefore arises why we lost air sacs in evolution. An obvious hypothesis would be that we lost them because of speech [9, 10]. However, in order to find an answer to this question, the potential acoustic function of air sacs must be understood.

In this paper a start is therefore made with modeling the acoustics of air sacs. The question that is investigated is, is: what would the acoustic effect be of an inflated air sac, connected to a vocal tract? Note that although the assumptions of an open connection to the vocal tract and of a passive function in vocalization are made, no claim is made in this paper that all primates always use air sacs in this way. Only the acoustic consequences of an air sac connected to the vocal tract are investigated. Whether air sacs are used in primate vocalizations at all, or whether primates can control the level of inflation and connection with the vocal tract, remains a question that needs to be investigated. However, with a detailed prediction of the acoustic effects of an air sac, such investigation might be facilitated.

Techniques from speech synthesis are a starting point for this modeling effort, but there are three potential differences between air sac models and models of the vocal tract. First of all, wall motion is of much larger influence on the acoustics of air sacs than it is on the acoustics of a vocal tract. This wall motion also increases the importance of acoustic energy radiated through the walls – an effect that is usually ignored in speech modeling. Finally, air sacs tend to have cross-sectional sizes that are comparable to those of the wave length of frequencies that are relevant to primate vocalizations. Therefore, the assumption that acoustic waves are flat, which is usually made in modeling the vocal tract, is no longer valid in modeling air sacs.

A first model is developed in some detail. This is a lumped element electrical analog model that is valid for lower frequencies. For higher frequencies (where the assumption of flat waves is no longer valid) a finite element model probably would probably be necessary but this is not elaborated in this paper. The lumped element model is used to investigate which factors have the most influence on the acoustics of an air sac. It is also shown how radiation through the walls of the air sac can be relevant at certain frequencies. The lumped element model is applied to approximate the spectrum of a howler monkey (*Alouatta guariba clamitans*) call, a spectrum that is difficult to explain with a simple tube model for the vocal tract.

2 Lumped element model

A lumped element model is a simplified representation of an acoustic system in which parts of the system are approximated by electronic components, such as capacitors, resistors or inductors. In such a system one electronic component often represents a spatially extended part of the acoustic system. This means that lumped element models are usually only good approximations at low frequencies – corresponding to wavelengths that are long in comparison with the dimensions of the modeled parts. However, as this approach simplifies the system to be modeled, analysis of a lumped element model can provide useful insights into the system's behavior.

The elements that are relevant for the acoustics of an air sac are the volume of air that resonates in the air sac, the wall that might vibrate and radiate sound, and the opening with which the air sac is connected to the rest of the vocal tract. Here we will not focus on how to model the connection, as it can be modeled by a standard acoustic tube model.

For the lumped element analysis, it will be assumed that pressure everywhere in the cavity of the sac is the same, that the wall moves with the same phase and amplitude everywhere, and that the air sac radiates sound as a sphere. The factors that are modeled are illustrated in Fig. 1.

2.1 The cavity

The air in the cavity acts as a spring that stores and releases energy when it is compressed and released. In electrical terms this can be modeled with a capacitor. As compressed air is heated slightly, and as this heat can be transferred to the walls, some losses might occur. This can be modeled by a (frequency dependent) resistor. The value of the capacitor, C_c in acoustic terms is given by:

$$C_c = \frac{V}{\rho_a c^2} \tag{1}$$

where V is the cavity volume, ρ_a is the density of air and c is the speed of sound.

The value R_c of the resistance due to losses at the wall is taken from Flanagan [1, section 3.24] and is given by:

$$R_c = \frac{\rho_a c^2}{A(\eta-1)}\sqrt{\frac{2c_p\rho_a}{\lambda\omega}} \tag{2}$$

where A is the cavity's area, η is the adiabatic constant, c_p is the specific heat of air at constant pressure, λ is the coefficient of heat conduction and ω is 2π times the frequency of vibration f. Values of all constants are given in table 1.

2.2 The wall

As for the motion of the wall, it will be assumed in the lumped elements approach to vibrate with the same amplitude and phase everywhere. It will also be assumed that it behaves as a damped oscillator, which is described by the following equation:

$$p(t)\cdot A = m\frac{dv}{dt} + bv + k\int v\,dt \tag{3}$$

where p is the differential pressure, v is the wall's velocity, m its mass, b its damping and k its stiffness. Differential pressure is the difference between the (vibrating) pressure in the air sac and the pressure of the air outside the air sac.

Now acoustic impedance is the ratio between pressure p and volume velocity $u = v{\cdot}A$. Rewriting Eq. (3) to volume velocity and solving for p gives:

$$p(t) = \frac{m}{A^2}\frac{du}{dt} + \frac{b}{A^2}u + \frac{k}{A^2}\int u\,dt \tag{4}$$

Now if p and u are harmonic vibrations, with angular speed ω, they can be written as:

$$p(t) = Pe^{i\omega t}, \quad u(t) = Ue^{i\omega t} \tag{5}$$

where P and U are the (complex) amplitudes of the vibrations. Substituting this in (4) and dividing out $e^{i\omega t}$ gives:

$$P = \left(\frac{m}{A^2}i\omega + \frac{b}{A^2} + \frac{k}{A^2}\frac{1}{i\omega}\right)U \tag{6}$$

This is equivalent to an inductance, a resistance and a capacitance in series. The mass, stiffness and damping can at least in theory be measured for any air sac. However, for the purpose of this paper it is more convenient if they can be calculated from the properties of the air sac wall tissue.

The wall's mass can be calculated from its area, its thickness and its density. This results in the following value for wall inductance L_w:

$$L_w = \frac{m}{A^2} = \frac{\rho_w dA}{A^2} = \frac{\rho_w d}{A} \tag{7}$$

where ρ_w is the density of wall tissue, and d is the wall's thickness.

The wall's stiffness depends on Young's modulus of the tissue. However, as the deformation of the wall is the stretching of a two-dimensional membrane, and Young's modulus is defined for stretching along one axis, Young's modulus E will have to be converted to a two-dimensional equivalent k_2 using Poisson's ratio ν:

$$k_2 = \frac{E}{2(1-\nu)} \tag{8}$$

This quantity gives a ratio between stretching of the surface and strain as follows:

$$k_2 = \frac{S/d}{\delta A/A} \tag{9}$$

where S is the surface tension, d the thickness of the wall, and δA the change in area. Now in order to find a relation between pressure and volume velocity (as is required for acoustic impedance) a relation between surface tension and pressure is needed, as well as a relation between change in area and volume velocity.

The relation between surface tension and pressure is given by the Young-Laplace equation:

$$p = S\left(\frac{1}{r_1} + \frac{1}{r_2}\right) \tag{10}$$

where p is the differential pressure, and r_1 and r_2 are the principal radii of curvature. For a spherical air sac, this simplifies to:

$$p = \frac{2S}{r} \tag{11}$$

In order to calculate the relation between change in area δA and volume velocity u, a relation between a radius of the air sac and its surface is needed. For all three dimensional shapes such a relation has the following form:

$$A = Cr^2 \tag{12}$$

where C is a constant that depends on the object's shape (4π for a sphere, for example). Now for a small change in area δA this becomes:

$$A + \delta A = C(r+\delta r)^2 \approx Cr^2 + 2Cr\delta r = A + 2Cr\delta r \tag{13}$$

For small values of δA and δr, such that second order terms in the small quantities can be ignored, the following relation therefore holds:

$$\delta A = 2Cr\delta r = 2A\frac{\delta r}{r} \tag{14}$$

or:

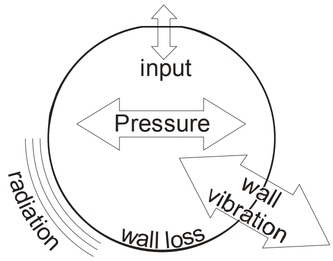

Fig. 1 Schematic representation of air sac, with modeled factors on the left and the lumped element electrical circuit on the right. Values for elements of the circuit are given in the text.

$$\frac{\delta A}{A} = 2\frac{\delta r}{r} \tag{15}$$

Finally, the total displacement of air (equal to the integral of volume velocity over time) is equal to A times δr. Substitution in (15) then gives:

$$\delta A = 2\frac{\int u dt}{r} \tag{16}$$

Taking (9), (11) and (16) together and solving for p finally gives:

$$\frac{4dk_2}{r^2 A}\int u dt = p \tag{17}$$

From this it follows that the capacitance of the wall in terms of properties of the tissue is:

$$C_w = \frac{r^2 A}{4dk_2} \tag{18}$$

Damping is more difficult to measure for tissue, and therefore the value for wall resistance is calculated indirectly [following 11]. Instead of measuring damping directly, the quality factor Q (a number that indicates how strongly a system is damped) of the whole system is estimated, and the wall resistance is calculated from the quality factor and the inductance and capacitance of the wall as follows:

$$R_w = \frac{1}{Q}\sqrt{\frac{L_w}{C_w}} \tag{19}$$

2.3 Radiation

For simplicity's sake it will be assumed that the air sac is a spherical radiator. This is admittedly quite unlike reality,

constant	value	parameter	value
c	350 m·s^{-1}	r	0.05 m
ρ_a	1.14 kg·m^{-3}	d	5×10^{-3} m
c_p	1.00×10^{3}J·kg^{-1}K^{-1}	k_2	9 000 Pa
λ	0.023 W·m^{-1}K^{-1}	ρ_w	10^3 kg·m^{-3}
μ	18.6×10^{-6} Pa·s	Q	1
η	1.4		

Table 1 Constants and parameters used in the lumped element model. Constants taken from [1, section 3.25].

but the relevant quantity is the amount of acoustic energy radiated per unit area, and this is not so different for different radiators. The spherical radiator results in the simplest equations. Furthermore, a hemispherical radiator in an infinite plane baffle (which is slightly more realistic) would result in the same radiation impedance.

The acoustical impedance Z_R of a spherical radiator is [e. g. 12, section 10.D.2b]:

$$Z_r = \frac{\rho_a c A}{1 + \frac{1}{ikr}} \tag{20}$$

where k is the wave number $2\pi f/c$. This is equivalent to a resistance:

$$R_r = \frac{\rho_a c}{A} \tag{21}$$

in parallel with an inductance:

$$L_r = \frac{\rho_a r}{A} \tag{22}$$

2.4 The complete circuit

Assuming that the pressure is equal in every part of the cavity, it follows that the air in the cavity is subjected to the same pressure as the inside of the wall. The outside of the wall is subject to the pressure outside which is given by the radiation load. Therefore an electrical circuit analog follows in which the cavity branch is parallel to the wall branch in series with the radiation load. This circuit is illustrated in Fig. 1.

2.5 Simplifying the circuit

Given the lumped element circuit, it is possible to figure out which factors dominate the circuit's behavior. For this, it is necessary to estimate a number of parameters, however. Some of these, such as the properties of air, are relatively well known, and need no discussion. Others, such as Young's modulus of tissue are less well known, but estimates can be found in the literature [e. g. 13]. A value of around 8.5 KPa for Young's modulus appears to be realistic. Given that biological tissue consists for a large part of fluids, and is therefore flexible but incompressible, Poisson's ratio must be 0.5 or slightly higher. This results in k_2 being approximately equal to Young's modulus, and therefore a value of 9 000 was used. A density of tissue of 10^3 kg·m^{-3} was assumed. Values for damping are harder to find in the literature, but in terms of the quality factor they range from 0.5 (which appears to be implicit in Maeda's vocal tract model [14]) to 10 [11]. Here, a quality factor of

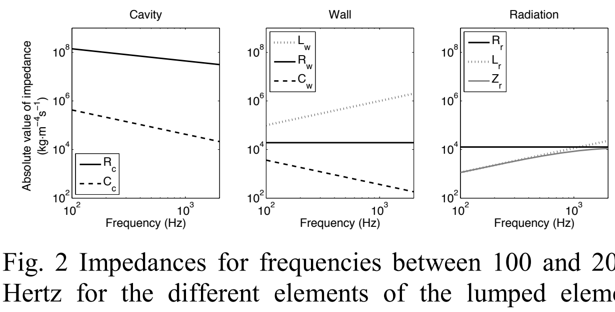

Fig. 2 Impedances for frequencies between 100 and 2000 Hertz for the different elements of the lumped element model.

1 has been used, assuming a relatively strong damping. This is justified by the fact that air sac walls are relatively thick and generally covered with hair. Finally, the radius of the air sac was chosen to be 5cm, its shape to be spherical and its walls to be 0.5cm thick.

The values of the different elements of the circuit were then calculated for frequencies between 100 and 2000 Hz (which is perhaps a somewhat larger range than for which the assumptions were valid). The results are shown in Fig. 2. Keeping in mind that parallel impedances are dominated by the lowest impedance, and series impedances are dominated by the highest impedance, it is clear that a good estimate of the total impedance of an air sac for the relevant frequency range can be obtained by only looking at the capacity of the cavity and the inductance (that is, the mass) of the walls. It can also be seen that exact values of stiffness and damping of the walls are not necessary for these simplifications to remain valid. This is in agreement with what Fletcher [11] has found when studying the inflated esophagus of the ring dove. However, as will be made clear in the results section, in order to understand sound production of vocal tracts with an air sac, for certain frequencies the amount of sound that is emitted is non-negligible, and therefore radiation has to be taken into account in that case.

3 Preliminary results

The final goal of modeling air sacs is to construct a complete vocal tract with an air sac. In order to do this, an air sac model, such as the one described above must be connected to an ordinary vocal tract model with a short tube. This is illustrated in Fig. 3.

The air sac and the connecting tube can then be modeled as a side branch of the vocal tract model. As supralaryngeal air sacs are connected to the vocal tract just above the glottis, strictly speaking they are not a side branch of the vocal tract, but a parallel branch. In electrical terms, this means that the air sac and the connecting tube form an impedance in parallel to the impedance of the vocal tract. This is illustrated in Fig. 3.

The impedance of an air sac with parameters given in table 1, and with a connecting tube with a diameter of 1cm and a length of 2cm is given in Fig. 4. It can be seen that the air sac impedance has a pole and a zero in the frequency range under consideration. The pole is caused by the resonance of the air sac wall and the air volume in the sac. The zero appears because the air sac and its connecting tube

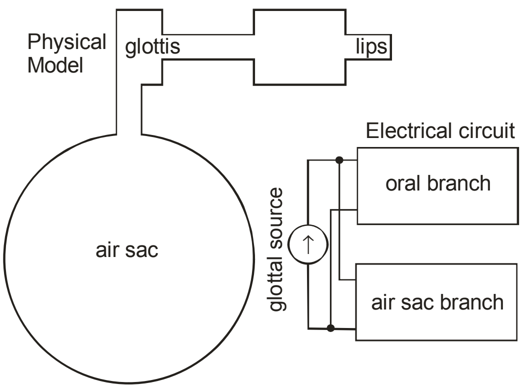

Fig. 3 The physical model (in "mid sagital" section) and the electrical circuit topology of a vocal tract with an air sac.

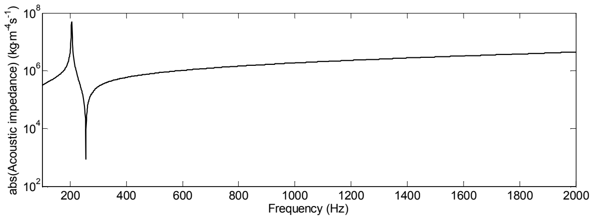

Fig. 4 Impedance of an air sac. Air sac dimensions are given in the text.

also act as a Helmholtz resonator. The pole-zero pair appears to be typical of an air sac, although their exact position varies with size.

Finally, it can be investigated what happens when an air sac is connected to a vocal tract. An example will be studied in some detail, as space is lacking for a more systematic exploration. However, the example has been selected to be biologically interesting, as it has a response function that is very similar to that of the howler monkey *Alouatta guariba clamitans*. The air sac dimensions are the same as before, and it was connected to a vocal tract of the shape shown in Fig. 3. The length of the tract was 11cm, and the radii of the cylindrical tubes making up the tract were 1.5cm for the wide tubes and 0.5cm for the narrow tubes. The lengths of the tubes had a ratio of 1:2:2:1 for a total length of 11cm. All the parameters are in the biologically plausible range for an animal the size of a howler monkey. The actual values however, are *ad hoc*, and not derived from real anatomical data. Potentially data from [15] could be used here, but those are from a different species than for which recordings were available.

Without an air sac, the vocal tract has formant frequencies of 433Hz and 947Hz. When an air sac is added, these frequencies shift up and a new peak appears at low frequencies. The result is shown in Fig. 5. In this figure the sound output of the tract with an air sac is compared with the sound output of a tract without an air sac. Also, the sound output at the lips and of the sac are shown separately for the tract with an air sac. It can be observed that the peak in the air sac's spectrum (Fig. 4) reappears in the total sound output. When one looks at the sound output at the lips, the valley in the air sac's spectrum also appears. However, here the air sac wall radiates sufficient sound to make this valley disappear in the total sound output. This results in a spectrum with three peaks at roughly 215Hz, 725Hz and 1215Hz. This corresponds qualitatively with a spectrum as measured from a howler monkey (*Alouatta guariba clamitans*), and which had peaks at around 300Hz, 750Hz and 1400Hz (Fig. 6). Another shared characteristic with the howler monkey spectrum is that no extra peaks appear at higher frequencies. Parameter tuning could undoubtedly improve the fit, and it is likely that an air sac

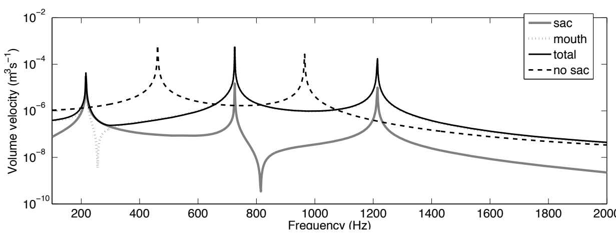

Fig. 5 Sound output spectra of the tract with air sac (and the contributions of sac and mouth separataly) and the sound output of the tract without a sac.

radius of 5cm is slightly too large to be realistic. A smaller air sac would increase the frequency of the first resonance.

5 Discussion and conclusion

A lumped element model of a supralaryngeal air sac has been presented. It has been shown that the acoustics are dominated by the volume of air in the air sac and by the mass of its walls, at least for biologically plausible dimensions and materials. It was also shown that with this model a reasonable approximation of the lower frequency characteristics of vocalizations of the *Alouatta guariba clamitans* could be given. This spectrum showed peaks at low frequencies that would correspond to a very long vocal tract if no air sac were present (a uniform tube of around 35cm would be needed to produce a similar spectrum).

However, the model in its present state is only valid for frequencies up to approximately 2000 Hz. Above these frequencies, the assumptions underlying the lumped element approach is no longer valid. In modelling ordinary vocal tracts, one would therefore switch to models consisting of multiple connected tubes. This is most likely not possible in the case of air sacs, because cross-sectional dimensions are in the same order as the wave lengths involved. The best candidate for modelling air sacs at higher frequencies is therefore most likely a finite element model. Such models can approximate any shape of object by splitting it up into a large number of simple elements. Such a model is under development. A disadvantage of finite element models is that they are very calculation intensive, however.

It should also be kept in mind that it is not claimed in this paper that all air sacs and all functions of air sacs in primates are acoustics and can be investigated with acoustic models. However, the model (or developments of it) proposed in this paper allows to rigorously test predictions of the acoustic effect of air sacs on vocalizations.

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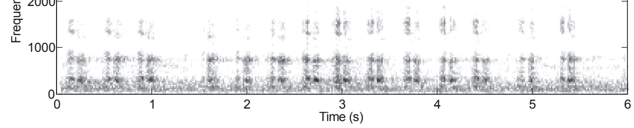

Fig. 6 Spectrogram of *Alouatta guariba clamitans* vocalization. Peaks are around 300, 750 and 1400 Hz.