VOCAL TRACT MODELING AS A TOOL TO INVESTIGATE SPECIES-SPECIFIC CUES IN VOCALIZATION

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Abstract: **Recent works emphasize the importance of acoustic cues of species-specificity in primate vocal communication. The potential of vocal tract resonance in generating these cues is examined by anatomically based vocal tract computational modeling. True lemurs (genus *Eulemur*), which occur in Madagascar, show a remarkable species diversity and this makes especially good model species to study these inter-specific differences. The oral vocal tract of lemurs is relatively flexible, but the nasal tract also plays a crucial role in their communicative system. We analyzed distinctive formant characteristics as produced by the computational models in order to investigate inter- and intra-specific variation in the vocal tract size and shape. Differences in morphological features between lemur *taxa* have an influence on shaping structural characters of their vocalizations.**

Keywords: **Prosimians, morphology, *Eulemur*, vocal behaviour.**

I. Introduction

The evolution of species-specific traits in communication signals is the result of complex interactions of neurocognitive and morphophysical factors.

In modern studies, the application of the source-filter model is central insight for the interpretation of mammal vocal production. The application of the source-filter model to non-human animals stressed the importance of formants in animal vocal communication [1][2].

Several studies demonstrated that formant-like band in animal sound are the products of the resonance of sound propagation in the vocal tract. [3][4]

However, the communicative importance of formants in non-humans is less manifest. Still little attention has been dedicated to the role formants play in conveying information. Researchers seem to agree on two kind of information conveyed: individual identity and body size.

The fact that formants are influenced by the length of the vocal tract [5], and thus by body size [6][7], was investigated in some recent studies and it has been demonstrated that birds and mammals can spontaneously perceive formants [8]. Hauser and Fitch [9] also suggested that communication via formants belonged to terrestrial vertebrates long time before the origin of humans. An open question is whether formants may play a role in conveying information on species specificity. Investigations of vocalizations in lemurs may have special importance because, even if DNA sequence analyses have yielded a broad consensus for phylogenetic relationships between *Eulemur*, *Hapalemur*, *Lemur* and *Varecia*, further relations between *taxa* are still controversial [10]. In fact, quantitative analyses of *Eulemur* species sounds are scarce, it is known that low-pitched sounds emitted by lemurs radiate from the nostrils [11] and that they possess species-specific acoustic features [12].

In this paper, we investigate the relevance of vocal tract morphology in determining differences in formant values and formant dispersion in the lemurs of Madagascar using vocal tract modelling, here applied to the study of resonances in the nasal airways.

II. Methods

One specimen per species for *Eulemur rubriventer*, *Eulemur macaco* and *Eulemur fulvus*, belonging to the collection of dead animals of Dept. Faune, Parc Botanique et Zoologique de Tsimbazaza (Antananarivo, Madagascar) were partially defrozen and tracheotomyzed. The tracheal tube was injected with silicon rubber until complete filling of the oral and nasal cavities, passing by the larynx, and then clamped. All length and dimension measurements of the cast were taken with a Mitutoyo digital caliper (accurate to 0.01 mm). Measurements of the cross-sectional axes of the vocal tract were then taken over the casts (the cross-section was not generally circular), at an increment of 10 mm. Cross-sectional areas were calculated starting from these measures in Microsoft Excel. Cross-sectional areas were used to build the vocal tract area function that represents the input of MatLab-based vocal tract modeling software [13]. Models of oral and nasal tract resonance in lemurs have successfully involved the use of concatenated tubes of varying cross-sectional areas [14].

Concatenated tube models of the nasal tract of each *taxa* were computed and the acoustic response was compared with formant measures taken from natural calls of the same species. Assuming that vocal tract morphology of a single dead animal's vocal tract is representative for each species, we also considered formants predicted by tubes in which size and length was respectively increased and decreased of 10%. Given that length scales as the cube root of mass, we estimated to

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take in account a body size variation of approximately 30%, reasonably larger than adult natural variation. For each model, F1 and F2 were taken in account from the computed acoustic response. Comparisons were made between F1 and F2 from the computed transfer functions and real formants for the same species measured on natural vocalizations. Captive lemurs were recorded in several institutions across Europe and United States: Parco Natura Viva (Bussolengo-Vr, Italy), Mulhouse Zoo (France), Rheine Der Naturzoo and Koln Zoo (Germany), Apenheul (Apeldoorn, The Netherlands), St. Louis Zoo (USA), Twycross Zoo, Drusillas Park (Alfrinston), Blackbrook Zoo (Alton Towers), Colchester Zoo, Linton Zoo and Banham Zoo (UK), Parc Botanique et Zoologique de Tsimbazaza (Antananarivo, Madagascar). All recorded vocalizations were spontaneously emitted and we avoided the use of eliciting stimuli and playbacks. Minimum of 3 vocalizations for 39 lemurs were digitized and analyzed using Praat 4.6.01 [15].

III. Results

We used the nasal tract length measurements from the 3 species to calculate expected formant values based on a simple tube model of the vocal tract [1][6][16]. The predicted formant values for a nasal tract length (Fig. 1) of 8 cm (congruent for *Eulemur rubriventer* and *Eulemur macaco*) are: 1094 Hz (F1) and 3281 Hz (F2). The predicted formant values for a nasal tract length of 9 cm (Fig. 1, resembling *Eulemur fulvus*) are: 972 Hz (F1) and 2917 Hz (F2).

Vocal tract area functions derived from the silicon cast were used to generate computational models for the nasal tracts of *Eulemur rubriventer*, *Eulemur macaco* and *Eulemur fulvus*.

The computational model for the supraglottal vocal systems of the three species considered in this paper comprises a filter consisting of 8 (*Eulemur rubriventer* and *Eulemur macaco*) or 9 (*Eulemur fulvus*) concatenated tubes. These tubes are approximation of the anatomical components of the vocal tract: from the glottal constriction, through the nasopharyngeal cavity, to the nasal chambers and nostrils. As from previous studies, non-human primates vocalize alternatively through the oral or the nasal tract [7][14].

Calculations of acoustic response can be made on the basis of the anatomically correct concatenated tubes model, where fixed-length tubes change in size according to anatomical measurements, whereas variation of these parameters allows their significance to be determined.

The acoustic response of the three nasal tract models showed differences between the species (Fig. 1): 472 Hz (F1) and 2276 Hz (F2) for *Eulemur rubriventer*, 1097 Hz (F1) and 2420 Hz (F2) for *Eulemur macaco*; 1005 Hz (F1) and 2263 Hz (F2) for *Eulemur fulvus*. Concatenated tubes models in which segments were increased or decreased of 10% in length and areas (in agreement with observed body size variation) respectively exhibited first peaks in the transfer function at: 447-532 Hz (F1) and 2074-2527 Hz (F2) for *Eulemur rubriventer*, 1010-1204 Hz (F1) and 2219-2664 Hz (F2) for *Eulemur macaco*; 918-1105 Hz (F1) and 2063-2508 Hz (F2) for *Eulemur fulvus*.

Comparisons were made between computed transfer functions and real formants for the same species. Average individual values of F1 and F2, measured from natural calls of 15 *Eulemur rubriventer*, 13 *Eulemur macaco* and 11 *Eulemur fulvus* specimens were then plotted with the acoustic output of the computational models (Fig. 1). Average F1 and F2 for *E. rubriventer* were 702 ± 176 Hz and 2576 ± 89 Hz respectively, F1 and F2 for *E. macaco* were 1311 ± 200 Hz and 2772 ± 117 Hz, 1082+300 Hz and 2249 ± 102 Hz *Eulemur fulvus*.

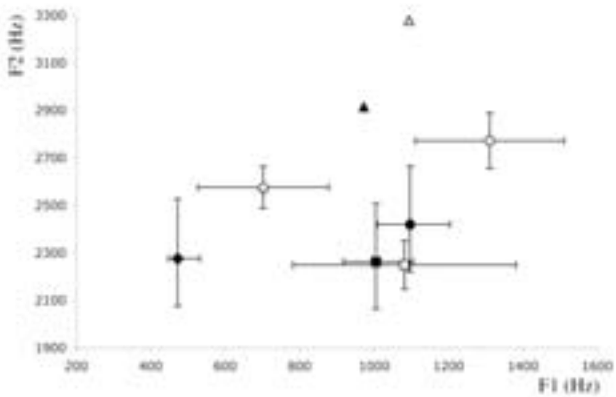

Fig. 1. Cumulative formant plot showing distribution of first (F1) and second (F2) formants: 8 cm (△) and 9 cm (▲) simple tube models; concatenated tubes model predictions for *Eulemur rubriventer* (◆), *Eulemur macaco* (●) and *Eulemur fulvus* (■); formants measured from natural calls for *Eulemur rubriventer* (◇), *Eulemur macaco* (○) and *Eulemur fulvus* (□).

IV. Discussion

Results presented in this paper are in agreement with previous investigations of lemur vocalisations, which have documented that resonance properties of the supralaryngeal tracts determine formants [14], which are useful to investigate differences between species.

First formant predicted from the computational models showed remarkable differences between *Eulemur rubriventer* and *Eulemur macaco*/*Eulemur fulvus*. Relatively minor differences were found between *Eulemur macaco* and *Eulemur fulvus*. Second formant of between *Eulemur rubriventer* and *Eulemur fulvus* are very similar and *Eulemur macaco* exhibited slightly increased values.

Computational models indicate that vocal tract morphology of *E. fulvus* and *E. macaco* proportionally varies in length and size of the concatenated tubes, while *E. rubriventer* actually showed a different formant pattern, reflecting remarkable discrepancies in the nasal tract morphology.

Observing formant variation in natural calls, it is possible to notice that all species tend to have greater variation than that predicted by the models, especially for F1. In agreement with model outputs, *Eulemur rubriventer* and *Eulemur macaco*/*Eulemur fulvus* showed remarkable differences for F1. The analysis of the natural calls also showed smaller variation than the models predicted and that F2 values well separated the three species.

A convincing explanation for differences between predicted and natural variation in the F1/F2 plot is that not all vocal tract morphological changes are strictly bound to body size variation. In particular, in some non-human primates species body size and vocal tract length show an allometric relationship and this can be well described in those sounds that allows a uniform tube model interpretation [6].

In those vocalizations that radiate through the nostrils, concatenated tubes models provided a more reliable prediction of F1 and F2 and the previous assumption does not imply that areas of the concatenated tubes proportionally vary with body size.

Unfortunately, a precise resolution of this issue was prevented by a lack of data documenting any disproportionate anatomical differences between males and females, or sub-adults and adults within a prosimian species [17].

V. Conclusion

Grunt vocalizations from three species of Madagascar lemurs showed consistent species-specific characteristics.

The results showed that a species-specific morphology of the nasal tract in some lemur species effectively determine formant frequencies in species-typical vocalizations. The degree of difference between species, as based both on the results of the acoustic analysis and on the acoustic response of vocal tract models changes in relation to the species.

Differences in morphological features between lemur *taxa* have an influence on specific structural characters of their vocalizations.

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