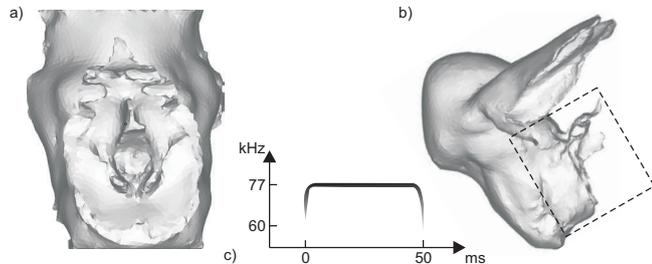


# On two possible mechanisms for call directionality steering in the rufous horseshoe bat, *Rhinolophus rouxi*

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**Figure 1:** a) Snout of the *Rhinolophus rouxi* (as used in the simulation) containing the noseleaf; b) 3D computer model of the *Rhinolophus rouxi*'s head with an indication of the part used in the simulation; c) Typical call of the *Rhinolophus rouxi* (Schematic spectrogram).

## Introduction

The *Rhinolophus rouxi*, or rufous horseshoe bat, is a member of the family of *Rhinolophidae*, the Horseshoe bats. This family of chiroptera occurs throughout the temperate and tropical zones of the Old World [1]. The *Rhinolophidae* usually emit echolocation calls through the nostrils, which are surrounded by a distinct noseleaf (see Fig. 1a.).

Being a CF-FM bat, the *Rhinolophus rouxi* has an echolocation call that consists of two components: a constant frequency (CF) and frequency modulated (FM) component. In particular, the CF part of the call, situated around 77 kHz and about 40 to 50 ms long, is preceded and terminated by a brief FM component (see Fig. 1c.). Based on observations of various *Rhinolophidae*, it is believed that the CF part of the call serves detection and identification of prey, as well as initial localization [2, 3]. The relative importance of the CF and FM portions during flight, in particular during the approach and terminal phase, is still debated. Recent results [4] indicate that the CF part of the call also plays a prominent function in the approach phase.

FM bats, i.e., bats whose echolocation calls mainly contain an FM component, were shown to rely on spectral cues for discriminating targets at different elevations (e.g. *Eptesicus fuscus* [5]). Those spectral cues are a result of the differences between the hearing-directionality patterns at different frequencies. CF-FM bats cannot exploit this effect for the CF portion of their call, as they only have one directionality. However, [6] showed that *Rhinolophus ferrumequinum* probably introduces directionality differences by means of stereotypical ear movements executed while echolocating. As argued in [7] this would allow them to localize targets in an analogous

fashion.

In this paper, we propose two other possibilities to introduce monaural directionality differences. As the echolocation system's directionality results of a combination from the hearing and sending directionality, affecting the call pattern could be as useful to a bat as affecting the hearing directionality. Hence, we put forward two hypotheses explaining possible mechanisms for call directionality steering: a noseleaf movement / deformation hypothesis, and a phase-change hypothesis.

The first hypothesis could be stated as follows:

Bats are able to contract and relax the muscles around the noseleaf. These contractions and relaxations result in noseleaf deformations or movement of the noseleaf, as well as in a nostril shape alteration. Modifying the noseleaf shape would result in changing the call directionality pattern. By applying those modifications simultaneous with their CF call an emission system with a time variant directionality is produced.

Although we have found no evidence of noseleaf movement in the *Rhinolophus rouxi*, it has been observed in other bat species.

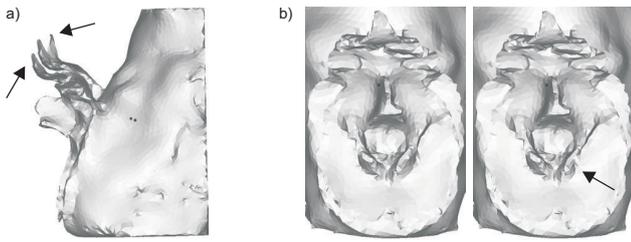
The second hypothesis is based on a common principle used in antenna design, the dipole antenna.

Nose-calling bats have a sound production apparatus with a call site consisting of two emitters, i.e., the nostrils. For a CF bat, those nostrils are horizontally spaced approximately half a wavelength of the CF portion of the call's frequency. This dipole configuration is often used in engineering to create an emitter with a specific directivity, consisting of a main lobe pointing forward with considerably smaller side lobes. Moreover, one can alter the direction of the main lobe by phase-shifting the emitted signals relative to each other. This specific emitter configuration would enable bats to alter the azimuthal properties of the call directivity.

In this paper, we test these two hypotheses using a Boundary Element Method simulation (BEM) [8].

## Moving the noseleaf

To investigate the first hypothesis, in which the bat deforms the noseleaf, moves it, or deforms the nostrils to generate a change in the emission pattern, we simulate



**Figure 2:** a) 3 noseleaf positions in which the call pattern is calculated (scanned position in the middle); b) left: scanned noseleaf; right: left nostril squeezed.

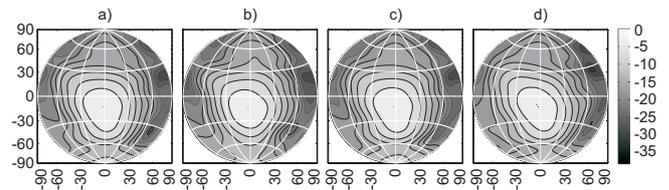
the various emissions patterns from the *Rhinolophus rouxi* following the procedure in [9].

A head of a *Rhinolophus rouxi* was scanned with a Skyscan<sup>1</sup> 1076 microCT scanner. After reconstruction of the slices with the reconstruction algorithm accompanying the scanner, Amira<sup>®2</sup> was used to generate a triangular mesh of the complete head's 3D surface model. This model contained over 1,000,000 triangles, but as the BEM simulator can only cope with approx. 35000 triangles, extra simplification was needed. Moreover, the BEM simulation requires the triangles to edge lengths smaller than  $1/6^{\text{th}}$  of the smallest simulated wavelength. Thus the ears and the back of the head were removed and the simulation was performed on a nose-only model (see Figs. 1a. and b.). To obtain the directionality, receivers were placed in the nostrils and sound sources were placed on the bat's frontal hemisphere (distance: 1 m).

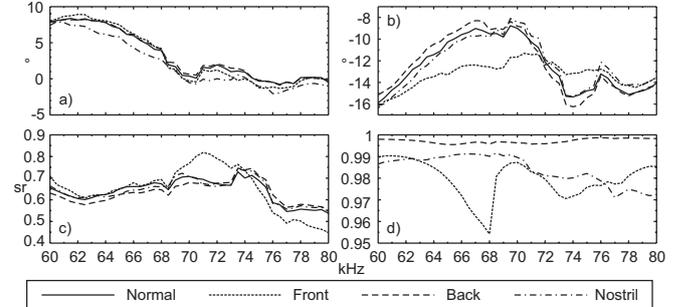
Four different models of the snout with noseleaf are considered: one in which the noseleaf is kept as scanned; a second model, contains a noseleaf flexed to the front; the third one has the noseleaf flexed to the back (see Fig. 2a.); in the last model one of the nostrils is deformed, i.e. the left nostril is squeezed (see Fig. 2b.).

Figure 3 displays the call directionality of the considered models at the CF-frequency of the *Rhinolophus rouxi* i.e., 77 kHz. Figure 3a. displays the directionality for the model in which the noseleaf is not altered with respect to the scanned data. The patterns exhibits features that are to be expected from a sound source consisting of two emitters in the horizontal plane who produce sound in phase with a spacing of about  $1/2$  of the wavelength: a main lobe pointing forward with a notch to the left and to the right. The elevation asymmetry results from the vertical asymmetry of the noseleaf. These properties are also present in the call directionality of a bat with a similar noseleaf, notably the *Rhinolophus ferrumequinem* [10].

In Fig. 3b and c. the patterns are shown for the model in which the noseleaf is flexed 1 mm towards the mouth of the animal and 1 mm backwards respectively. They are similar to the original one qualitatively as well as quantitatively. The downward pointing sidelobe (around  $90^\circ$  elevation) shifts slightly down and up respectively.



**Figure 3:** Call patterns at 77 kHz: a) scanned position; b) flexed to the front; c) flexed to the back; d) left nostril squeezed.



**Figure 4:** FM sweep comparisons over frequencies: a) main lobe azimuth evolution in  $^\circ$ ; b) main lobe elevation evolution in  $^\circ$ ; c) main lobe solid angle evolution; d) correlations between the directionalities of the model as scanned and the deformed models.

Finally the left nostril is reduced about 50% in width. From Fig. 3d. we conclude that the directionality remains roughly the same. A small azimuthal asymmetry is introduced, which might be useful for localization purposes, if it is sufficiently large for the range of biologically plausible contractions. More research is needed on this topic.

Summarizing, we conclude that the call directionality at the frequency of the CF portion of the bat's call is not significantly affected by the proposed noseleaf deformations. However, since the bat emits short frequency modulated sweeps at the beginning and/or the end of its call (in the interval 60 - 77 kHz), we also investigate the influence of the noseleaf and nostril deformations on the call directionality at these frequencies. Figures 4a., b., and c., which display the primary characteristics of the main lobe (-3 dB contour, as in [9, 11]), indicate that they are similar for most frequencies. The correlation coefficients displayed in Fig. 4d. ( $\geq 0.955$  for all frequencies) further corroborate our conclusion that the deformations have only a small effect on the directionality for all frequencies.

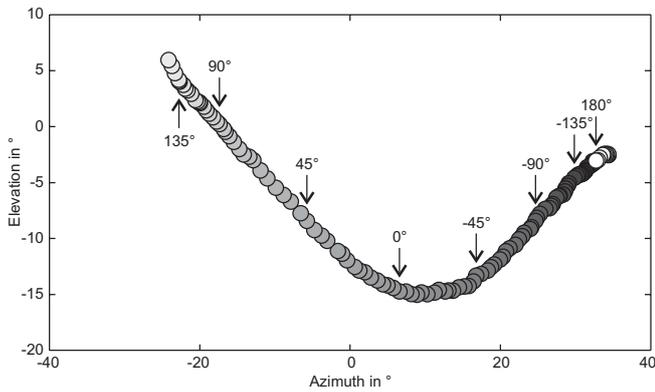
As no evidence is available to decide whether the proposed noseleaf deformations occur at all or whether the effect of the modelled deformations corresponds with reality, this hypothesis is very speculative. More detailed measurements of vocalizing CF bats are needed. The present simulation results, however, indicates that the use of noseleaf deformations for call directionality steering is unlikely.

## A dipole emitter

In this section, we propose another mechanism for the bat to produce enhanced call directionality during the

<sup>1</sup>www.skyscan.be

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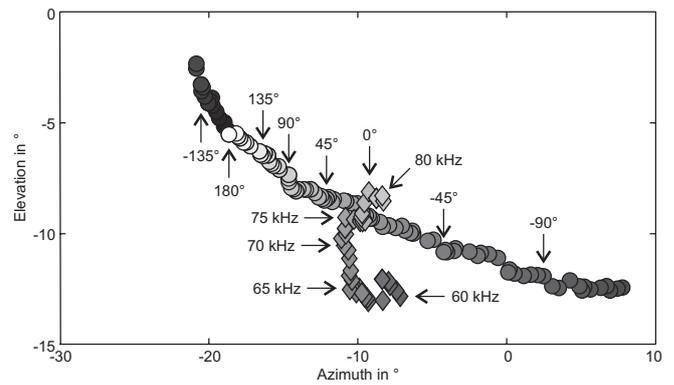


**Figure 5:** Main lobe azimuth and elevation location of the sending pattern in a horseshoe bat (*Rhinolophus rouxi*) performing a phase sweep.

CF part of its call. The call generation site of the bat (the two nostrils) is a dipole with the elements in the horizontal plane. Moreover, the spacing between the elements is approximately half a wavelength of the emitted frequency. Such an array can conveniently be used to perform beam steering, effectively changing the azimuth location of the main lobe [12]. This beam steering results from changing interference patterns of the signals sent from the two nostrils when changing the relative phase of those signals.

Figure 5 plots the location of the call's main lobe's centroid during the spatial sweep that is performed when altering the phase of the signal coming from the left nostril from  $-180^\circ$  to  $+180^\circ$  (from dark dots to lighter dots) while keeping the signal from the right nostril at  $0^\circ$  phase. This figure shows evidence that endorses our second hypothesis, since the azimuth sweep spans approximately  $60^\circ$ . This is significantly higher than the azimuth sweep the bat could achieve in the FM part of the call (approx.  $7^\circ$ , see Fig. 4a.). A very interesting additional phenomenon introduced by this phase-sweep, is the main lobe's changing elevation. It even surpasses the elevation span of the beam sweep introduced by the FM portion of the call (phase-induced span: approx.  $21^\circ$ ; FM-induced span: approx.  $8^\circ$ , see Fig. 4b.). This effect is due to the complex shape of the noseleaf, which results in complex interference patterns rather than in a straightforward dipole interference pattern.

To assess the practical applicability of the phase-sweep-induced spatial scanning in the echolocation system, combining the sending with the receiving directionality is essential. Figure 6 shows the spatial location of the main lobe of the convolution of the directivity pattern of the phase-shift-induced sweep with the left ear. This figure indicates that both the phase-shift-induced azimuth and elevation sweeps in the call directionality are maintained when convolving with the head related transfer function (HRTF). The final main lobe covers a smaller range due to the ear's directivity pattern, which is the same for all phase shifts. (Az. span: call only = approx.  $60^\circ$ , convolution with HRTF = approx.  $30^\circ$ ; El. span: c.o. = approx.  $21^\circ$ , c.w.h. = approx.  $11^\circ$ , see Figs. 5 and 6



**Figure 6:** Main lobe azimuth and elevation location of the echolocation pattern (sending pattern convolved with the left ear's HRTF) in a horseshoe bat (*Rhinolophus rouxi*). Diamonds: the locations for frequencies between 60 and 80 kHz ( $0^\circ$  phase shift emission) perceived at the left ear. Circles: the locations for the phase differences at 77 kHz perceived at the left ear.

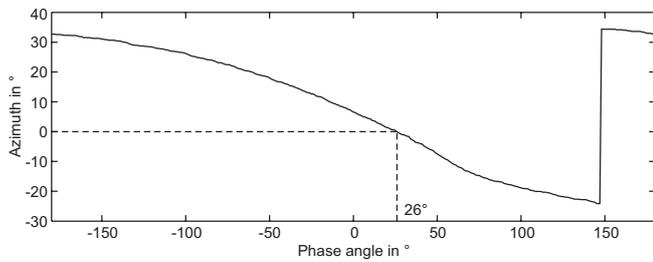
(circles)).

To grasp the importance of the spatial extent over which the echolocation system's main lobe sweeps when applying a phase shift, a comparison is made with the main-lobe's evolution in the FM-part of the *Rhinolophus rouxi*'s call (see Fig. 6). The system's main lobe traverses a wider azimuth region in the phase-swept CF portion of the call than in the ordinary FM portion of the call (CF: approx.  $30^\circ$ ; FM: approx.  $7^\circ$ ). Moreover, the elevation information, which is generally accepted as being coded in the monaural system for FM bats, is also present in the phase-swept CF portion of the call: The elevation extent of the main lobe sweep is similar for both the FM part as the phase-swept CF part, even slightly bigger latter (CF:  $11^\circ$ ; FM:  $8^\circ$ ).

In summary, we conclude that employing phase sweeps during the CF portion of the call could be at least as effective as having a regular FM-call pattern. In particular the introduction of a spatial azimuth sweep could be beneficial to the bat's localization capabilities.

Even if the phase-induced sweeps would turn out not to be used for localization, bats could possibly employ a phase shift for another reason. To be of most use to the widest range of tasks the main lobe from the call directionality should point forward (in the mid-sagittal plane). However, the presence of slight asymmetries in the shape of the noseleaf could point the beam outside of this plane. Enforcing a compensating phase shift between the signals from the two nostrils during the CF portion of the call could compensate for this and realign the main lobe with the mid-sagittal plane.

Fig. 7 displays the azimuth scan of the call directivity's main lobe in relation to the phase difference between the nostrils (left - right). As can be seen in this figure, for the scanned specimen the main lobe points to  $+7^\circ$  without any phase difference between the signals sent from both nostrils. A constant phase delay of  $26^\circ$  imposed on the signal emitted from the left nostril with regard to the



**Figure 7:** The azimuth location of the main lobe in the sending pattern for a horseshoe bat (*Rhinolophus rouxi*) in function of phase delay between the sound emitted from the right and the left nostril.

signal sent from the right nostril would realign the main lobe with the forward direction again.

Consequently, phase alteration of the signals emitted through the individual nostrils could be able to enhance the bat's localization capabilities in two ways. Firstly, by passing through the complete phase difference range from  $-180^\circ$  to  $180^\circ$  (or a subset hereof), or secondly by imposing a constant phase delay on one of the nostril's signals to maintain a forward pointing beam.

## Conclusions

For CF/FM bats to steer their call directionality during the call, we proposed two methods: the first one uses noseleaf or nostril deformations, the second one introduces phase sweeps between the signals emitted through the nostrils.

Despite the fact that noseleaf deformations are not documented in the *Rhinolophus rouxi*, they were observed in other noseleaved bats, such as the *Phyllostomus discolor*. However, our simulation results suggest that biologically plausible deformations of the noseleaf have only a minimal effect on the call directionality.

Concerning the introduction of the phase sweeps, more indications have been found that this method improves the localization capabilities of the bat. Moreover, correction of main lobe deflection in azimuth due to asymmetries can be achieved with a constant phase delay between the signals sent from both nostrils. It remains to be seen, however, whether such phase steering is actually used by bats.

In absence of evidence in the literature that bats can independently drive the signals at the two nostrils, the analysis described above is still hypothetical. We conjecture that phase steering might be possible by contracting muscles in the nose cavities, but experimental evidence for such a mechanism still needs to be gathered.

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