Numerical Analysis of the Bat Noseleaf Dynamics and its Impact on the Encoding of Sensory Information

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Numerical analysis of the bat noseleaf dynamics and its impact on the encoding of sensory information
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(ABSTRACT (academic))

Echolocating bats use biosonar as the primary far sense to collect information about the environment. This information is encoded at the baffle structures – noseleaves (emission) and pinnae (reception) – that act as interfaces between the biosonar system and the external world. The baffles have complex static geometry and can undergo rapid, non-rigid shape deformations while diffracting the outgoing/incoming sound waves. These shape deformation are a result of specific muscular actuation and can be controlled by bats. However, the functional significance of these shape deformations to the performance of biosonar system is unclear. The current work primarily focuses on: i) the study of the impact of noseleaf dynamics on the outgoing sound waves, ii) the study of the impact of baffle dynamics on encoding of sensory information and localization performance of bats. For this, we use digital models of the horseshoe bat noseleaf that were computer animated to recreate noseleaf dynamics as observed in bats. The beampatterns for the noseleaf models were numerically predicted and evaluated using an information-theoretic approach. The following findings were obtained: i) there was an interaction between lancet dynamics (a part of the noseleaf) and furrows (local shape feature). The forward lancet rotations increased the amount of sound energy allocated to secondary amplitude maxima (sidelobes) in the beampattern, but only in the presence of the furrows, ii) the baffle dynamics results in encoding of new sensory information, iii) the variability in encoded sensory information similar for frequency and baffle dynamics and iv) the new sensory information encoded improved the performance of biosonar on two sensing tasks namely direction resolution and accuracy of direction-finding. These results affirm the importance of dynamics in biosonar system of horseshoe bats and point at the possibility of biosonar dynamics as a key factor behind the astounding sensory capabilities of these animals that are not yet matched by engineering systems. Thus, these biosonar dynamic principles can help improve the man-made sensing systems and help close the performance gap between active sensing in biology and in engineering.
Numerical analysis of the bat noseleaf dynamics and its impact on the encoding of sensory information

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(ABSTRACT (public))

Horseshoe bats possess a sophisticated biosonar system that helps them to negotiate complex unstructured environments by relying primarily on the sound as the far sense. For this, the bats emit brief ultrasonic pulses and listen to incoming echoes to learn about the environment. The sites of emission and reception in these bats are surrounded by baffle structures called “noseleaves” and “pinnae (outer ears)”. These are the only places in the biosonar system where direction-dependent information gets encoded. These baffle structures in bats unlike the engineering systems like megaphones have complex static geometry and can undergo fast deformations at the time of pulse emission/reception. However, the functional significance of the baffle motions in biosonar system is not known. The current work primarily focuses on: i) the study of the impact of noseleaf dynamics on the outgoing sound waves, ii) the study of the impact of baffle dynamics on encoding of sensory information and localization performance of bats. For this, we take a numerical approach where we use computer-animated digital models of bat noseleaves that mimic noseleaf dynamics as observed in bats. The shapes are acoustically characterized (beampatterns) numerically using a finite element implementation. These beampatterns are then analyzed using an information-theoretic approach. The followings findings were obtained: i) noseleaf dynamics altered the spatial distribution of energy, ii) baffle dynamics results in encoding of new sensory information, and iii) the new sensory information encoded due to baffle dynamics significantly improves the performance of biosonar system on the two target localization tasks evaluated here – direction resolution and direction estimation accuracy. These results affirm the importance of dynamics in biosonar system of horseshoe bats and point at the possibility of biosonar dynamics as a key factor behind the astounding sensory capabilities of these animals that are not yet matched by engineering systems. Thus, these biosonar dynamic principles can help improve the man-made sensing systems and help close the performance gap between active sensing in biology and in engineering.
Dedicated
to my
beloved family
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Chapter 1

Introduction

This chapter introduces the principles and advantages of the bat biosonar over technical systems including the dynamic aspect of bat biosonar system that is the focus of current research. Additionally, discussed here are the goals and approach taken for the current research.

1.1 Bio-inspired science and technology

Bio-inspired science and technology is an interdisciplinary field of study at the intersection of biology, engineering and physical sciences. It seeks to understand the biological function perfected by nature over billions of years through evolution and use the gained insights in the design of man-made systems. This study of animate systems as a source of inspiration to design man-made systems ranging from architecture to technological systems is not new and has already resulted in significant advances in the fields such as surface coating (e.g., self coating Lotusan paint [1]), dry adhesion [2], sensing (e.g., motion sensor of optical mouse [3]).
The critical reasons behind the superior performance of biological systems is functional integration across multiple levels as well as biological organization. Biological materials, for example, get their functional properties from the structural features that exist at the nano- and micro-scale as well as macroscopic scale. In similar fashion, the function of many biological structures can only be understood from their specific behavioral, ecological and evolutionary contexts. Thus, one of the challenges for the future development of bio-inspired field is to bring the principles of multi-level functional integration and organization to design of man-made systems.

Animal biosonar (e.g. bats, dolphins) systems are analogous to the technical sensing systems such as radar and sonar in certain contexts. Traditionally, the contexts in which such systems (radar, sonar) have operated share little with the conditions under which animal biosonar operates. The differences has been in speeds and scale of operation along with the environment in which either system operates. However, in last few years advances in the autonomous robotic platforms for operation in air and underwater environments have spurred interest in study of animal biosonar systems. Such robotic systems like micro-air vehicles (MAVs) are intended to operate in small-scale and structure-rich environments analogous to those inhabited by bats. Currently, there exists a large performance gap between the capabilities of bats and that of technical systems. Bats are able to travel long distances in night through structure-rich dense vegetation at high speeds \([4]\) while successfully avoiding obstacles and performing other navigation tasks reliably. Bats excel from technical systems in speed, versatility and reliability with lesser amounts of inputs data.

Previous research in bat biosonar has given insights into important aspects of biosonar but the reasons behind superior biosonar performance continue to elude. In this work, we look at the conspicuous dynamics present in bat noseleaves – fleshy structures that surround the nostrils in nasal emitting bats – and their functional significance in bat biosonar system.
Furthermore, we investigate the impact of noseleaf and pinnae dynamics on the performance of bat biosonar system on two sensing tasks namely direction-resolution and accuracy of direction-finding.

1.2 Bat biosonar system as a model

Bat biosonar is a sophisticated system with adaptation at multiple levels and hence encompasses a diverse set of acoustic systems to suit diverse perceptual problems encountered by bats [5]. Bats make up about 20% of all existing mammals and have about 1200 known species that have evolved in a rapid diversification over time [6, 7, 8]. Out of these 1200 species, approximately 1000 bat species use laryngeal echolocation as their primary far sense [9]. The biosonar system in these bats operates in one of the two modes: i) active mode: analyze the returning echoes triggered from their own ultrasonic vocalizations or ii) passive mode: analyze the incoming sounds from foreign sources to gather information. Using both active and passive biosonar modes, bats have been able to occupy diverse habitats and exploit diverse variety of foods that include nectar, pollen, fruit, insects, arthropods, fish, small terrestrial vertebrates, birds, other bats and blood from large vertebrates [10, 11].

An example of an adaptation in biosonar system is design of biosonar pulses. Based on their time-frequency structure biosonar pulses can be broadly classified as frequency modulated (fm, see Fig. 1.1(a)), constant frequency-frequency modulated (cf-fm, see Fig. 1.1(b)) or combinations of these two [12, 13]. Foraging bats use one of these biosonar call types based on the perceptual problems they encounter while foraging. The perceptual problems differ based on the habitat, food type and hunting mode (e.g. gleaning or hunting flying insects) as well as the echolocation task at hand i.e. detection, classification or localization [5]. For example, the long cf signals in combination with Doppler-shift compensation and specialized
hearing system are extremely good in detection of weak echoes emanation from fluttering insects in a cluttered environment [5, 14] while broadband FM signals are good for exact target localization [5].

![Biosonar call types: a) Frequency modulated (fm), b) Constant frequency-frequency modulated (cf-fm).](image)

Another important adaption in biosonar system is in the morphology of outer structures that surround the site of emission and reception (see Fig. 1.2). In most bat species, ultrasound is produced by the larynx, propagates along the vocal tract and finally comes out of the nostrils (nasal emission) or mouth (oral emission). In the case of nasal emission, the nostrils are frequently surrounded by prominent baffle structures called “noseleaves” [15]. Similarly in case of oral emission, baffle structures surround the mouth. These baffle structures are often intricately shaped structures adorned by flaps, ridges, and furrows and their geometry determines an acoustic diffraction process which is responsible for the spatial distribution of the emitted ultrasound [15, 16, 17]. This ability of noseleaves to alter the distribution of emitted sound energy spatially may pay a role in the encoding of sensory information about the environment. Similarly, the site of reception is surrounded by morphologically diverse outer ears (pinnae) [18] (see Fig. 1.2). The outer ears form the first stage of mechano-electrical transduction process that transforms incoming sound pressure waves into neural action potentials for internal signal processing and thus may play a role in the encoding of
salient sensory information about the environment [19, 20].

![Figure 1.2: Examples of noseleaf and pinnae diversity in echolocating bats: (a) Stoliczka’s trident bat (*Aselliscus stoliczkanus*), (b) serotine bat (*Eptesicus serotinus*), (c) pipstrelle bat (*Pipistrellus sp.*), (d) great roundleaf bat (*Hipposideros armiger*), (e) mouse eared bat (*Myotis sp.*), (f) greater horseshoe bat (*Rhinolophus ferrumequinum*).](image)

The ability of bats to adapt to diverse perceptual problems that they encounter combined with demonstrated superior performance with minimal input (two one-dimensional signals) makes bat biosonar system an attractive model for improving technical sensory systems. The adaptability of bat biosonar systems comes from species-level adaptations. These biosonar adaptations optimized to perceptual problems encountered in a particular ecology and can be attributed to adaptive radiation over millennia. However, such species-level adaptations alone can’t explain the superior performance that bats demonstrate over man-made sensing systems when operating in complex and unstructured environments. It is thus likely that bats have evolved mechanisms to encode relevant sensory information to perceptual problems they face. These mechanisms, however, remain unknown to engineering.
1.3 Dynamics in bat biosonar system

Evolutionary adaptation has allowed for species-level adaptations in bat biosonar system optimized to address specific perceptual problems. One such adaption in bat biosonar system is dynamics associated with the outer structures – noseleaves and pinnae – of bat biosonar system [16, 21, 22]. Such dynamic shape manipulations have no equivalent in man-made sensing systems.

Previous studies have shown that noseleaves and pinnae in horseshoe and old-world roundleaf nosed bats can undergo fast, non-rigid deformations (family Rhinolophidae [7] and Hipposideridae [7]). These dynamic shape changes are facilitated by specific muscular actuation and occur during the emission/reception of biosonar pulses [16, 21, 22](see Fig.s 1.3, 1.4).

Noseleaves and pinnae form the interfaces between the biosonar system and the external world. They form the substrate for encoding of direction-dependent information and hence their beampatterns (input/output gain as a function of frequency and direction) represent a view of the environment. Thus, to adapt the beampatterns to current needs is very critical for bats. This can be done by either: i) a change of wavelength of biosonar pulses or ii) a change of shape geometry. The shape dynamics allows for the ii) as shown by previous studies [22, 16, 17] (see Fig.s 1.4, 1.5). and thus have an impact on the sensory perception of bats [23].
Figure 1.3: Deformation pattern of the anterior leaf of the greater horseshoe bat (*Rhinolophus ferrumequinum*): a) anterior leaf motion detected by laser, b) geometry of anterior leaf, c) simultaneous sound pressure, anterior leaf movement velocity and displacement measurements. Reproduced from [21]. See page 1 of copyright permissions document.

Figure 1.4: Deformation pattern and numerical study of the lancet of the greater horseshoe bat (*Rhinolophus ferrumequinum*): a) high-speed video recording sequences of lancet movement, b) time window of the pulse period and lancet motion, c) simulation results of the bending lancet effect on the beampattern. Reproduced from [16]. See page 1 of copyright permissions document.
Figure 1.5: Deformation pattern and numerical study of the pinna of the greater horseshoe bat (*Rhinolophus ferrumequinum*): a) high-speed video recording sequences of lancet movement, b) time window of the pulse period and lancet motion, c) simulation results of the pinna dynamics on the beampattern.
1.4 Research objectives

The work presented in this dissertation is aimed at gaining a deeper understanding of the noseleaf shape dynamics as observed in the horseshoe bats and its use as a substrate for encoding of sensory information. To this end, four fundamental questions were asked:

1. What is the relationship between noseleaf geometry and its acoustic properties? This is of interest as noseleaves act as the interface between bats and the surrounding. The noseleaves by means of acoustic diffraction, control the spatial distribution of emitted ultrasonic sound, thereby controlling the way the bat perceives the surroundings.

2. How does the noseleaf dynamics impact the emitted ultrasound? Of particular interest is the impact on encoding of sensory information.

3. What role do conspicuous local shape features play in the context of dynamic changes of overall noseleaf shape?

4. Do bats gain in terms of performance improvements over just the static noseleaf geometry as a result of dynamics?
1.5 Research approach

For current work, we pursued a numerical approach for the study of noseleaf shape dynamics. This approach was pursued as in-depth and in-vivo analysis of noseleaf is difficult primarily because of: i) complicated noseleaf geometry and ii) complex & fast noseleaf deformation patterns that are hard to repeat in an identical fashion in a behaving bat.

For numerical studies, the horseshoe bat noseleaf digital models were obtained through \( \mu \)CT scans of the adult bat specimens. The digital models were then computer animated to recreate the dynamics as observed in behaving bats. The three-dimensional models were then posed into different shape configurations and characterized acoustically through a finite-element formulation.

This approach not only removes the difficulties associated with behavioral experiments, but also offers a number of distinct advantages:

1. Easy to manipulate digital models and test multiple configurations that comprise of motions in individual noseleaf parts and their interactions.

2. Ability to predict acoustic near-field along with far-field (beampatterns). This allows for an understanding of underlying physical mechanisms behind the observed effects of static geometry & dynamics on beampatterns.

3. Ability to test configurations that are not observed in bats, but still could be insightful and lead to interesting technical solutions.
1.6 Research Contributions

The specific contributions of this dissertation are summarized below. This dissertation shows that:

1. Noseleaf dynamics allows for an active control of the spread of the emission beam by a spatial redistribution of energy in horseshoe bats.

2. Biosonar dynamics is a novel way to generate diverse beampatterns in environments less conducive to broadband signals.

3. Biosonar dynamics helps bats to encode additional sensory information that improves the performance of bat biosonar system.

Figure 1.6: Typical workflow of the biosonar research: Work highlighted in red focus of current research.
Chapter 1. Introduction

dissertation

1.7 Chapter outline

The remaining chapters in this document have been organized as follows:

Chapter 2 describes the methods used to obtain animated digital noseleaf models – that mimic motion dynamics as observed in bats – from bat specimens.

Chapter 3 describes the numerical technique used for the acoustic characterization of digital noseleaf models.

Chapter 4 presents the results obtained from the numerical simulations and discusses the interplay of lancet dynamics and local shape features (i.e. furrows).

Chapter 5 presents the results obtained from the numerical simulations and discusses the variability in sensory information encoded through just use of lancet dynamics or frequency.

Chapter 6 discusses the performance improvements in localization tasks achieved due to shape dynamics using an information-theoretic based analysis of data.

Chapter 7 summarizes the work performed for this dissertation and presents suggestions for the future work.
Chapter 2

Digital noseleaf models

This chapter describes the methods used for obtaining digital noseleaf models from bat specimens and subsequent rigging of the digital models to recreate noseleaf dynamics as observed in bats.

2.1 Three-dimensional digital models

The adult horseshoe bat specimens for the present analysis were taken from caves in China. The specimens were housed in the lab and were fed a diet of mealworms. The noseleaf motions were recorded using high-speed video cameras [24].

The noseleaf digital models were obtained by scanning post-mortem samples of noseleaves through X-ray computer tomography (Skyscan 1172 \texttrademark{} CT). To get the models, X-ray images of the noseleaf samples were acquired from directions that spanned a total of 180° in steps of 0.45°. The X-ray images were then converted into a stack of tomographic cross-sections using cone-beam reconstruction method. These cross-section images recorded X-ray absorption in
isotropic pixels (35μm edge length) at a resolution of 8 bits/pixel (256 gray levels). The images were first pre-filtered using hand-editing of pixels and Gaussian smoothing kernel and then thresholded to classify pixels as either representing air or noseleaf tissue. After thresholding, the resulting binary voxel representation was converted to three dimensional polygonal surface mesh using marching cubes algorithm. The noseleaf meshes were then cleaned of reconstruction artifacts like noise spikes using shape-base smoothing algorithms (Smooth & Polish brushes, ZBrush4R4, Pixologic). Finally, the meshes were treated for mesh quality issues like webbing and holes using polygon editing tools (Bridge & Topology pens, Modo601, Luxology) [24].

2.2 Animated digital models

The treated digital noseleaf models were then computer-animated (rigging) to recreate noseleaf dynamics as observed in behaving bats. To mimic the noseleaf motions in digital models required the following: i) For simple motions like bending, a skeleton with control points and joints was attached to noseleaf mesh (Maya2013, Autodesk) (see Fig. 2.2) and ii) For complex motions like altering the size of furrows, blendshapes were used that morphed portions of the models to match individually sculpted alterations. The final animated noseleaf model had multiple degrees of freedom to mimic noseleaf motions (see Fig. 2.3) [24].

For acoustic characterization, noseleaf was posed into different configurations and the resulting meshes were converted to binary voxel representation. The voxel representation was then down-sampled and transcribed into a finite-element mesh for numerical simulations [24].
Figure 2.1: The shape of the studied noseleaf and its parts: a) Photo of the individual of the greater horseshoe bat (*R. ferrumequinum*), b) Surface rendering of the noseleaf model using a triangular mesh. The different parts of the noseleaf are (1) lancet, (1a) upper furrow, (1b) lower furrow, (2) sella, (3) anterior leaf (c) Photo of the individual of the old world leaf-nosed bat (*H. armiger*), (d) Surface rendering of the noseleaf model using a triangular mesh. The different parts of the noseleaf are (1) posterior leaf, (1a) furrows, (2) anterior leaf.
Figure 2.2: Digital noseleaf model (greater horseshoe bat, *Rhinolophus ferrumequinum*). To mimic the dynamic changes in noseleaf shape observed in bats, the digital models were rigged for animation by setting up a skeleton with joints (circles) and links (triangles). a) front view, b) side view. Reproduced from [25].
Figure 2.3: Manipulations of the digital noseleaf model of horseshoe bat: a) shape configuration of the sample in the original (upright) configuration as obtained from the $\mu$ CT scan, b) anterior-posterior rotation of the lancet, c) furrows filled. Reproduced from [17]. See page 2 of copyright permissions document.
Chapter 3

Acoustic characterization

This chapter describes the numerical technique used for the acoustic characterization of
digital noseleaf models.

3.1 Numerical simulation

The numerical approach for acoustic characterization of digital noseleaf models was pursued
for two reasons: i) it is easy to manipulate digital models and test multiple configurations
that are comprised of motions of individual parts and their interactions and ii) the ability to
predict the acoustic near-field (see Fig. 3.1(c)) along with a far-field characterization (beam-
patterns) (see Fig. 3.1(b)). The numerical model used here consisted of three components:
(i) finite elements, (ii) infinite elements, (iii) a projection based on the Kirchhoff integral.
The finite element mesh consisted of linear cubic elements, the geometry of which was a
natural match for the voxel-array format of the micro-CT data from which the meshes were
derived. The meshes were sampled at a spatial resolution of 0.0715 mm which corresponds
to element densities from 60 (80 kHz, wavelength $\lambda = 4.3$ mm) to 81 (60 kHz, $\lambda = 5.8$ mm) per wavelength. The finite element mesh was used to obtain a numerical estimate of the complex near-field amplitudes within a cuboid that enclosed the immediate vicinity of the surface of the noseleaf or ear. The domain of the finite-element mesh was set up to extend at least two wavelengths from the surface of the biological specimen.

This distance was chosen to allow the infinite elements (s. below) to simulate propagation out into the free field accurately; it was not intended to extend the finite-element computation out into the far field, since the latter was done computationally more efficiently using the Kirchhoff integral formulation (s. below).

The finite element formulation was constructed to find a numerical solution to Helmholtz differential equation [26]:

$$\nabla^2 \Phi + k^2 \Phi = -b,$$

\hspace{1cm} (3.1)

Finite element analysis (FEA)

Figure 3.1: Schematic of acoustic characterization of digital noseleaf model using numerical technique: a) Digital model of horseshoe bat ($R. ferrumequinum$), b) Acoustic near-field at 80 kHz, c) Acoustic far-field (beampattern) at 80 kHz derived by projecting acoustic near-field to a set of points on the sphere as shown in (b). The color coding is linear and represents acoustic gain.
where $k = \frac{2\pi f}{c}$ is the wavenumber, $b$ the force term representing acoustic source placed in each nostril [8], $c$ the speed of sound in $m/s$, and $f$ the frequency in kHz. The surfaces of the noseleaves or pinnae were modeled as perfectly reflecting.

The element stiffness matrices $K_{el}$ for the geometry of the finite element mesh representing the air volume were determined by an analytical evaluation of the expression:

$$K_{el}^{ij} = \Delta K_{el}^{ij} - k^2 \Delta M_{el}^{ij} = \int_{V_{el}} \nabla N_i^T \nabla N_j - k^2 N_i N_j dV,$$  \hspace{1cm} (3.2)

where $K_{el}^{ij}$ are the entries of element stiffness matrices, $\Delta M_{el}^{ij}$ the entries of the acoustic element mass matrix, $N_i$ the $i$th shape function, and $V_{el}$ is the volume of the element. All $K_{el}^{ij}$ are real numbers. The acoustic stiffness and mass matrices are independent of frequency. The element stiffness matrix is same for all elements in the regular cubic finite-element mesh. The shape functions attached to the cubic elements of the finite-element mesh were linear.

The outer boundary of the finite-element computational volume was covered with a single layer of three-dimensional mapped wave envelope infinite elements [27] to simulate reflection-free outward propagation of the sound into the free field. The element stiffness matrices for the infinite elements were determined by evaluation of the expression:

$$K_{el}^{ij} = \Delta K_{el}^{ij} - k^2 \Delta M_{el}^{ij} + jk \Delta C_{el}^{ij},$$  \hspace{1cm} (3.3)

where $j$ is the imaginary unit and $\Delta C_{el}^{ij}$ is the damping term. In the radial direction, Jacobi polynomials of order three with parameters $\alpha = 2$ and $\beta = 0$ were used [28] as shape functions. The shape functions for the infinite elements were integrated numerically using Gauss-Legendre quadrature.

To obtain the near-field amplitudes, the linear problem defined by the stiffness matrix and
the force matrix was solved iteratively at the element nodes using a biconjugate gradient stabilized method (BGSM) \cite{26, 29, 30} with a successive over-relaxation preconditioner. The preconditioner’s splitting matrix $Q$ is given by

$$Q = \frac{1}{\omega}D - C_l$$

where $D$ is the diagonal matrix of the system matrix (master stiffness matrix), $C_l$ its strictly lower triangular portion, and $0 < \omega < 2$ the relaxation factor (set to a value of 1.2). The implementation of the linear system solving routines was taken from the Portable, Extensible Toolkit for Scientific Computation PETSC software library \cite{31}.

The far-field directivity estimates (beampatterns) used to acoustically characterize the nose-leaf digital models were computed using a Kirchhoff integral formulation \cite{26, 32, 33, 34}:

$$\Phi(\hat{\mathbf{x}}) = -\frac{1}{4\pi} \int_S \frac{e^{jkR}}{R} \hat{n} \left[ \nabla \Phi + jk \left( 1 + \frac{j}{kR} \right) \frac{\hat{R}}{R} \Phi \right] ds,$$

where $R$ is the vector between surface element $ds$ and position $\hat{\mathbf{x}}$, $\hat{n}$ the outward surface normal, $\Phi$ the field value on $S$ and $k$ is the wavenumber. The product $\hat{n} \cdot \nabla \Phi = \frac{\partial \Phi}{\partial \hat{n}}$ is the derivation of the field $\Phi$ w.r.t. the surface normal $\hat{n}$ evaluated numerically by a three-point difference spanning the outer three layers of the finite-element mesh \cite{26}.

The Kirchhoff method assumes that all sound sources, scattering surfaces, and non-linear effects are contained with the surface over which the integration is carried out \cite{34, 35}. It does not assume that the integration surface is located in the near-field and can hence be used for predictions of near- as well as the far-field values \cite{33}.

To arrive at a beampattern estimate, the Kirchhoff integral method was used to project from near-field amplitudes onto a set of points that were placed on the surface of sphere
with a radius of 1 m. This distance was chosen to fall well outside of the near-field far field boundary. The magnitude of the projected field was normalized over all directions for each frequency \( f \). The normalized real-valued directivity was given by \( 0 \leq D(\theta, \phi, f) \leq 1 \) [26].

Kirchhoff integral methods (KIM) have been extensively used in electromagnetic problems, aeroacoustic problems as well as wave propagation problems in acoustics. Some examples are: 1) KIM used to predict electromagnetic radiation far-field from simple dipole antenna. The near-field here is computed using finite-difference time-domain (FDTD) methods [33], 2) KIM used to simulate supersonic jet noise with near-field computed using computational fluid dynamics (CFD) techniques [36] and 3) KIM used to simulate noise propagation from a driven cavity in far-field where near-field was computed using computational fluid dynamics (CFD) techniques [37].

An alternate approach based on boundary element method (BEM) has also been used for acoustic characterization of noseleaf models previously [38]. The noseleaf beampatterns predicted using BEM approach and the Kirchhoff integral based approach pursued here were found to be qualitatively similar.

To further validate the method, the predicted beampatterns for simple monopole and dipole sources were compared to those predicted analytically. The numerically predicted beampatterns were found to match the ones predicted analytically.

As a final step to validate the beampatterns, the numerically predicted beampatterns were compared to the beampatterns measured using a physical noseleaf prototype. The physical noseleaf prototype was fabricated from an elastic material using 3D printing (Objet 3D printer) techniques. The geometry of the physical prototype came from the \( \mu \)CT scan of post-mortem noseleaf sample. Thus, the prototype replicated the noseleaf in life-like geometrical detail. The prototype was scaled to twice the size of the noseleaf to ease handling and
to allow the use of lower frequencies. The prototype was actuated by a simple linear actuator (Firgelli L12-1). The actuator applied a force from behind to bend the lancet of the noseleaf forward mimicking the motion observed in bats. The actuator motors had a latency of 300 ms and a maximum linear velocity of 23 mm/s to carry out the motion during or between the emission of biosonar pulses. The ultrasonic pulses were produced by a capacitive ultrasonic loudspeaker (Ultra Sound Advice S56, diameter 50 mm) that was coupled to the nostrils using a waveguide (tapered cone connected to two flexible tubes to interface with nostrils). As input to the system, a chirp signal was used that was generated digitally. After conversion, the signal was amplified by an analog amplifier and sent to the loudspeaker. The acoustic signal then propagated through the waveguide, was modulated by the local deformation of noseleaf and was recorded by a pressure-field microphone (Brüel & Kjær 4138 1/8”) in the far-field about 1 m away from the loudspeaker [24]. To get beampatterns, the noseleaf was fixed on an artificial head made out of styrofoam. The head helped support the noseleaf, block motor noise and direct reflections away from the noseleaf. The whole setup was mounted on a pan-tilt unit (FLIR Motion Control System PTU-D48E), which provided 180° azimuth and 120° elevation rotation with a rotation step size of 3° to assess the emitted sound-field as a function of direction [24]. These measured beampatterns on comparison with numerically predicted beampatterns were found to be qualitatively similar, validating the numerical method described here.

3.2 Acoustic source configuration

(This section was published in Proceedings of Meetings on Acoustics (POMA), June, 2013, doi: 10.1121/1.4800656. Reproduced with permission [8]. See page 3 of copyright permissions document.)
In echolocating bats, the ultrasound is produced by the larynx that propagates along the vocal tract and finally comes out of the nostrils or mouth. The site of emission – mouth or nostrils – are frequently surrounded by conspicuous fleshy structures called “noseleaves”. For the acoustic characterization of noseleaves numerically, the vocal tract where the actual excitation takes place is only partially included or left out completely. The acoustic source is instead placed in the nasal tubes, slightly upstream of nostrils. This limits the size of the model and computational effort associated with numerical predictions. However, this way of excitation differs from the in-vivo excitation and demands an investigation into the potential impact of alternate excitation modes on numerical beampattern predictions. To so this, a series of experiments were performed with differing excitation modes and the resulting beampattern predictions were compared to those obtained from a complete shape model that included a partial vocal tract.

3.2.1 Methods

Two noseleaf samples samples from adult old world leaf-nosed bats (Hipposideros armiger, see Fig. 3.2) were used for the present analysis. Both samples were taken from freshly collected specimens and stored in low-concentration (about 10%) ethanol until the tomographic scans could be performed. The specimens scanned consisted of complete bat heads, with pinnae removed and their noseleaves intact and in a shape configuration that was free of any noticeable post-mortem artifacts. Similarly, the vocal tract was preserved in its life-like form. Three-dimensional models of the noseleaf geometry were obtained by X-ray microtomography (Skyscan 1172: Bruker µCT, Kontich, Belgium). Starting from these complete models, different shape configurations and source placements were created by hand-editing the voxels. There were four configurations that were tested. In first configuration (case 1) sound sources were placed in each of the nasal tubes such that there was no path difference
between them. For second & third configurations (case 2 & 3), the path difference between the sources was increased to $\lambda_{\text{min}}/8$ & $\lambda_{\text{min}}/4$ respectively, where $\lambda_{\text{min}}$ is 4.95 mm (70kHz). For the fourth configuration (case 4), the source was placed in the vocal tract 4 mm from the location of the start of vocal tract (see Fig. 3.3). For all experimental configurations, the acoustic near field inside a cuboid-shaped volume surrounding the noseleaf was predicted using a finite element model consisting of linear cubic elements derived directly from the voxel shape representation. The forcing vector of the model was set up to simulate either a point source placed in the vocal tract or two point sources placed in each of the nasal tubes of the noseleaf. Frequencies spanning the entire frequency range (54 to 70 kHz in 2kHz steps) known to be covered by biosonar pulses’ second harmonic [39] were analyzed. The beampattern estimates spanned 360° in azimuth and 180° in elevation with an angular resolution of 1°.

### 3.2.2 Results

The beampattern predictions obtained for both samples showed a dependence on the source position selected for the different simulations: For sample 1, the beampatterns for case 1 (zero path difference between sources) showed a single main lobe wider in azimuth than elevation at lower frequencies with no side lobes. At higher frequencies, however the beam widened in elevation more than in azimuth with a side lobe that appeared to break away from main lobe. For case 2 ($\lambda_{\text{min}}/8$ path difference between sources), beampatterns showed a single main lobe wider in elevation than azimuth at lower frequencies. In the medium frequency range, the main lobe split into two lobes but combined into one again at higher frequencies. There was, however, no fully separated side lobe. As the path difference was increased between sources in case 3 ($\lambda_{\text{min}}/4$ path difference between sources), the split became more pronounced and spanned the entire frequency range. Finally, when a single source was placed
Figure 3.2: Surface renderings of the analyzed shapes (polygonal meshes): a) sample 1 without vocal tract, b) sample 2 without vocal tract, c) sample 2 with vocal tract. Reproduced from [8]. See page 3 of copyright permissions document.
Figure 3.3: Placement of the sound sources for the different simulations: a) configuration with two numerical sound sources (S1 & S2) placed in the nasal tubes, the parameter of these simulation is the distance between the sources d. d takes values of 0 (case 1), $\lambda_{\text{min}}/8$ (case 2), $\lambda_{\text{min}}/4$ (case 3), where $\lambda_{\text{min}}$ is 4.95 mm (70kHz), b) configuration with a single sound source (S) placed 4mm from the point of the start of vocal tract (case 4). Reproduced from [8]. See page 3 of copyright permissions document.

in the vocal tract 4 mm from the point of the start of vocal tract, the split disappeared and the beampatterns showed again a single main lobe without a clear side lobe.

The beampatterns for sample 2 (see Fig. 3.5) were qualitatively very similar to those of sample 1 (see Fig. 3.4) except that split of the main lobe into two lobes in case 2 was much more prominent in sample 2 than sample 1 and spanned the entire frequency range.
Figure 3.4: Comparison of beampattern estimates for sample 1 for the four different combinations of the location of placement of sound sources: a) Beampatterns for case 1 with no path difference between sources b) Beampatterns for case 2 with $\lambda_{\text{min}}/8$ path difference between sources c) Beampatterns for case 3 with $\lambda_{\text{min}}/4$ path difference between sources d) Beampatterns for case 4 with source in the vocal tract 4 mm from the start of vocal tract. The amplitude is linearly encoded in colored scale, where red represents the maximum value. Reproduced from [8]. See page 3 of copyright permissions document.
Figure 3.5: Comparison of beampattern estimates for sample 2 for the four different combinations of the location of placement of sound sources: a) Beampatterns for case 1 with no path difference between sources b) Beampatterns for case 2 with $\lambda_{\text{min}}/8$ path difference between sources c) Beampatterns for case 3 with $\lambda_{\text{min}}/4$ path difference between sources d) Beampatterns for case 4 with source in the vocal tract 4 mm from the start of vocal tract. The amplitude is linearly encoded in colored scale, where red represents the maximum value. Reproduced from [8]. See page 3 of copyright permissions document.
3.2.3 Discussion

The results obtained in the present study strongly suggest that the placement of sources in numerical simulations used to predict the beampatterns of noseleaves can have a major impact on the results. This was found to be true in the cases where the vocal tract had been removed from the sample geometry and two sources were used to emulate the sound coming out of the two nostrils. In these cases, the positioning of the two sources can be critical: If the two sources are placed at different depth inside each nasal tube, this can result in the formation of multiple lobes in the beampattern that are were not seen with a single source placed down inside an intact vocal tract. These split beam are thus likely to be artifacts. These artifacts can be avoided - even in the two-source configuration without a preserved vocal tract - if care is taken to position both sources at an even depth inside each nasal tube. The present findings can thus be seen as evidence that simulations of noseleaf patterns without vocal tract and two sources placed in the nasal tube can produce valid results and hence it is not necessary to increase the computational problem to include the entire vocal tract.
Chapter 4

Interplay of lancet furrows and shape change in the horseshoe bat noseleaf

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This chapter discusses the impact of noseleaf dynamics on beampatterns and the interaction between lancet, component of noseleaf and furrows (local shape feature of noseleaf).

4.1 Abstract

Horseshoe bats emit biosonar pulses through the nostrils and diffract the outgoing ultrasonic pulses with baffles, so-called “noseleaves”, that surround the nostrils. The noseleaves have complex static geometries and can furthermore undergo dynamic shape changes during emission of the biosonar pulses. The posterior noseleaf part, the lancet, has been shown to carry out anterior-posterior flicking motions during biosonar emissions with average lancet tip displacements of about one millimeter. Here, the acoustic effects of the interplay between the lancet furrows and shape change (lancet rotation) on the emission beam were investigated using the animated digital models obtained from the noseleaves of greater horseshoe
bats (*Rhinolophus ferrumequinum*). It was found that forward lancet rotations increase the amount of sound energy allocated to secondary amplitude maxima (sidelobes) in the beampattern, but only in the presence of the furrows. The interaction between static and dynamic features can be readily quantified by roughness (standard deviation about local mean) of the amplitude distribution of the beampatterns. This effect goes beyond the static impact of the furrows on the width of the mainlobe. It could allow the bats to send out their pulses through a sequence of qualitatively different beampatterns.

4.2 Introduction

Horseshoe bats (family Rhinolophidae) are a group of bats that are known for a sophisticated biosonar system that is adaptive at multiple levels. Some of the noteworthy adaptations of horseshoe bat biosonar are in signal design (narrow-band pulse segments, high-duty cycle pulse trains [5, 40]), cochlear signal processing (acoustic fovea [41, 42]) as well as in a rapid and adaptive control of the carrier frequency (Doppler-shift compensation [43]). In addition to these adaptations, horseshoe bats – along with the closely related Old-world leaf-nosed bats (family Hipposideridae) – form one of two major bat groups that emit their ultrasonic pulses through the nostrils with calls composed primarily of constant frequency (CF) component with narrow frequency modulated (FM) components at the initial and the terminal portions. Like in other nasally emitting bats, the nostrils in horseshoe bats are surrounded by conspicuous fleshy baffle structures known as "noseleaves" that diffract the outgoing ultrasonic waves. In horseshoe bats, the noseleaves exhibit a particularly complex geometry that can be broadly broken up into three parts: i) the anterior leaf, a horseshoe-shaped baffle surrounding the nostrils, ii) the sella, a peg positioned in the center of the noseleaf posterior of the nostrils, and iii) the lancet, a triangular flap at the posterior of the
noseleaf characterized by four half-open cavities referred to as “cells of the lancet” or simply “furrows” (see Fig. 4.1) in many horseshoe bat species.

An impact of the lancet on the distribution of the emitted ultrasonic energy over direction (beampattern) has already been suggested in early work by Schnitzler & Grinnell [44] who covered the upper part of the noseleaf with petroleum jelly (vaseline). They reported merging of the mainlobe & sidelobe and change in the mainlobe direction from pointing in the flight direction to 30° below it as a result of covering the lancet. In addition to this, they also suggested an increased diffusion of energy in azimuth (horizontal) and decrease in diffusion of energy in elevation (vertical). However, since the exact changes to the lancet geometry were not documented in these early experiments and the beampatterns were not recorded as a function of frequency, these results cannot be used to infer a detailed link between form and function.

The first detailed acoustic analysis of the lancet was presented by Zhuang & Müller [26] and used numerical simulations based on a three-dimensional digital shape model for the noseleaf of a rufous horseshoe bat (Rhinolophus rouxi). The results suggested that furrows act as half-open resonance cavities that effect the width of the beam, in particular, in the low-frequency subband that is covered by the frequency modulated (fm) portion of the biosonar pulse. A similar study in the same bat species by Vanderelst et. al. [38] confirmed the impact of the furrows on beamwidth but reported an opposite direction for the effect. Whereas Zhang & Müller [26, 45] reported that the furrows widened the beam, Vanderelst et. al. [38] found a narrowing.

Recent research results have suggested that apart from their static geometric complexity, baffle structures of horseshoe bats also have a conspicuous dynamic dimension to them. This dynamic dimension is due to fast, non-rigid deformations of the noseleaf shapes that are brought forth by muscular actuation and happen on time scales that are similar to the
durations of individual ultrasonic pulses and echoes [16, 21]. It has been shown that the anterior leaf in greater horseshoe bats (*Rhinolophus ferrumequinum*) can undergo inward twitching motions in tight correlation with emission of the biosonar pulses. These motions produced overall changes to noseleaf geometry by altering the curvature of noseleaf’s walls that led to overall changes in the size of the noseleaf aperture of up to one fourth of a wavelength. It remains unknown, however, if the deformations of the anterior leaf have any functional significance to biosonar system [21]. Similarly to the anterior leaf, the lancet has been shown to exhibit an anterior-posterior flicking motion during biosonar pulse emission that resulted in an average displacement of the noseleaf tip by about one millimeter [16]. Numerical simulations performed on digital noseleaf shapes that were manipulated to recreate the lancet rotations digitally have produced evidence for a considerable effect on the shape of the emission beam [16].

The goal of the work presented here has been to investigate the role of the furrows on the ultrasonic emission beam in the context of a noseleaf that incorporates the lancet shape dynamics reported by He *et al.* [16]. In doing so, an emphasis has been placed on analyzing a set of samples with sufficient size to ensure the robustness of the observed effects against individual variability and hence go beyond the single shape samples that have been the basis of the previous studies [26, 38, 45]. The research presented here was based on digital shape models of the noseleaves. The lancet dynamics was recreated in these models using digital animation techniques [24].

### 4.3 Quantitative analysis of beampatterns

For the present analysis, three adult greater horseshoe bats (*Rhinolophus ferrumequinum*) were taken from caves in the vicinity of Jinan, Shandong Province, China. A three-dimensional
Figure 4.1: The shape of the studied noseleaf and its parts:
a) Photo of the individual of the greater horseshoe bat (*R. ferrumequinum*). The shape of the studied noseleaf and its parts: a) Photo of the individual of the greater horseshoe bat (*R. ferrumequinum*), the species from which the analyzed noseleaf models were derived. b) Surface rendering of the noseleaf model using a triangular mesh. The different parts of the noseleaf are: 1) lancet, (1a) upper furrow, (1b) lower furrow, (2) sella, (3) anterior leaf. The total height of the modeled noseleaf is about 11.5 mm and the furrows in the lancet are approximately 1.4 mm wide and deep. Reproduced from [17]. See page 2 of copyright permissions document.
surface mesh model representation of the noseleaf samples from these bats was obtained using X-ray microtomography (Skyscan 1072; Bruker µCT, Kontich, Belgium). The 3d digital noseleaf models were then treated for reconstruction artifacts & mesh quality issues. After this clean-up, the models were rigged for animation by setting up a skeleton with control points and joints to mimic the lancet motions seen in bats (Maya2013, Autodesk, see Fig. 4.2, [24, 16]).

After rigging, the noseleaf models had two degrees of freedom: i) anterior-posterior flicking motion of the lancet and ii) opening-closing of the furrows (see Fig. 4.3). Using these degrees of freedom, the 3d models were posed into different shape configurations. The lancet was rotated from an upright position to being bent forward 10° in steps of 5° and for each lancet position cases with open and closed furrows were created. For each shape model, predictions of the acoustic near-field were obtained numerically using a finite-element formulation [45, 26]. For the finite-element simulations, the structures were sampled at a spatial resolution of 0.0715 mm which corresponds to element densities from 60 (80 kHz, wavelength $\lambda = 4.3$ mm) to 81 (60 kHz, $\lambda = 5.8$ mm) per wavelength. The complex near-field amplitude values were used to obtain far-field beampattern estimates using a projection method based on the Kirchhoff integral [45, 26]. All these numerical analysis steps were carried out for five equidistant frequencies across the bats’ biosonar broadcast frequency range (60-80 kHz).

To analyze the effect of lancet rotation and furrows on emission sound field, the beampatterns were characterized by histogram estimates of the probability density functions (pdfs) of the beampattern amplitudes. The amplitude pdfs were computed for individual frequencies and for pooled beampattern amplitudes across entire biosonar broadcast frequency range (five equidistant points between 60-80 kHz) for each noseleaf configuration. The computed pdfs of the amplitudes were then used to study the occurrence of amplitudes peaks among the
Figure 4.2: Digital noseleaf model (greater horseshoe bat, *Rhinolophus ferrumequinum*). To mimic the dynamic changes in noseleaf shape observed in bats, the digital models were rigged for animation by setting up a skeleton with joints (circles) and links (triangles). a) front view, b) side view. Reproduced from [17]. See page 2 of copyright permissions document.
higher amplitudes of the beampatterns (see Fig. 4.4). For this purpose, higher amplitudes were defined as values above the median gain. From the pdf estimates, a moving average was computed using a rectangular window with a length of 11 histogram bins. The moving average was then subtracted from the original pdf estimate to detrend the data and leave only the variation about the mean. To quantify the amount of variation in the pdf estimates obtained for different noseleaf configurations and frequencies, a roughness coefficient ($R_{RMS}$, [46]) was calculated for the detrended estimates as:

$$R_{RMS} = \sqrt{\frac{1}{n} \sum_{i=1}^{n} y_i^2}. \quad (4.1)$$

where $n$ is number of peaks and $y_i$ is the height of the $i^{th}$ peak.

The peaks were identified by finding local maxima in the amplitude pdfs. A peak detected was retained only if it was larger than five data samples on either side. Also, peaks that

Figure 4.3: Manipulations of the digital noseleaf model: a) shape configuration of the sample in the original (upright) configuration as obtained from the $\mu$ CT scan, b) anterior-posterior rotation of the lancet, c) furrows filled. Reproduced from [17]. See page 2 of copyright permissions document.
were closer than five data samples to each other were dropped to filter small peaks closer to larger and prominent peaks.

![Diagram](Image)

Figure 4.4: Method to estimate amplitude pdf roughness: a) pdf with median marked with gray line, b) pdf truncated at the median, c) truncated pdf smoothed using a box window, d) peaks in the pdf isolated by subtracting smoothed truncated pdf (c) from original truncated pdf (b), smoothed using a box window and peaks marked with gray solid circular markers. Reproduced from [17]. See page 2 of copyright permissions document.

### 4.4 Results

The beampatterns predicted for all samples (see Fig. 4.5) showed that the natural (open) state of the furrows was responsible for narrower beams. Filling the furrows resulted in an average increase of $16^\circ$ (29%, standard deviation $\sigma = 4^\circ$) in elevation and $11^\circ$ (28%, $\sigma = 1^\circ$) in azimuth of the -3 dB bandwidth. This effect was observed across all lancet rotations (see Fig. 4.6).
The pooled beampattern amplitude pdfs, for the open-furrow models, showed distinctive local peaks in the range of higher amplitudes (larger than the median gain, see Fig. 4.7). The number of these amplitude peaks increased substantially with increasing lancet rotation down from the upright position (see Fig. 4.7, left-hand column). For all lancet configurations other than the upright position, filling the furrows resulted in the disappearance of the local peaks in the pooled amplitude pdfs. The peaks in the amplitude histograms were found to correspond to beampattern amplitudes located on the slopes of the mainlobe as well as in sidelobes, i.e., separate secondary maxima. Over 70% of the beampattern amplitudes in these peaks were found to fall in the frontal hemisphere of the beampattern. The difference in the prominence of local peaks was found to be reflected in the pdf roughness ($R_{\text{RMS}}$). For the upright position of the lancet ($0^\circ$), the $R_{\text{RMS}}$ values showed that filling of furrows resulted in an increase in pdf roughness. However, on lancet rotation, this trend reversed itself and filling of furrows resulted in the disappearance of peaks and consequently a reduction of $R_{\text{RMS}}$ for these lancet configurations. In the upright condition, filling the furrows increased $R_{\text{RMS}}$ by an average of 16% ($\sigma = 6\%$). At a lancet rotation of $5^\circ$, it resulted in an average decrease in $R_{\text{RMS}}$ of 7%($\sigma = 3\%$). At $10^\circ$, the effect of filling the furrows got even stronger and result in a 22% ($\sigma = 7\%$) decrease in roughness (see Fig. 4.8).

The individual frequency pdfs, similar to pooled pdfs showed local distinctive peaks in the range of higher amplitudes. Because of the large variability in pdf roughness ($R_{\text{RMS}}$) across frequency, the overall trends shown in Fig. 4.8 were not visible in many of the individual frequencies, but emerged only once the entire frequency band was considered.
Figure 4.5: Numerically predicted beampatterns for bat noseleaf model 1: Each row shows different lancet positions & corresponding furrow configuration. Each column shows different frequencies. The gray level coding of amplitudes is logarithmic and the level of mainlobe contour line is at -3dB. Reproduced from [17]. See page 2 of copyright permissions document.
Figure 4.6: Extension of main beam on furrow filling across different lancet rotations: a), b) & c) show beamwidth data for three noseleaf digital models. The left and right columns show azimuth and elevation beamwidths respectively calculated at -3dB level. The solid lines represent beamwidths for furrow open and dashed line for furrow filled configurations. □: Lancet in upright position, ◊: Lancet rotated in anterior-posterior direction by 5°, ◆: Lancet rotated in anterior-posterior direction by 10°. Reproduced from [17]. See page 2 of copyright permissions document.
Figure 4.7: Comparison of amplitude pdfs (model1) for furrow open and furrow filled configurations across different lancet rotations. The amplitude pdfs were constructed by pooling the data across frequency. Reproduced from [17]. See page 2 of copyright permissions document.
Figure 4.8: Comparison of amplitude pdf roughness coefficient ($R_{RMS}$) estimates. Each bar denotes the change in pdf roughness coefficient ($R_{RMS}$) on filling of furrows from furrow open configuration for different lancet configurations. Reproduced from [17]. See page 2 of copyright permissions document.
4.5 Discussion

The data presented here confirms that the static effect of the lancet furrows is a narrowing of the beam (by approximately 29\%) in elevation and azimuth across the bats’ biosonar frequency range (60-80 kHz) as reported by Vanderelst et. al. [38]. Since the present result was found to be consistent across all three noseleaf samples, it is likely that the beam widening reported by Zhuang and Müller [26] was either due to an outlier sample or a mix up of data sets.

The observed systematic changes in roughness of the amplitude pdfs of the beampatterns were a property of the entire frequency band used by horseshoe bats, but were highly variable from frequency to frequency. Hence, the roughness measure is a feature of a change to the overall input that a horseshoe bat would receive across all its frequency channels as it changes the orientation of its lancet. The observed interaction changed the beampatterns significantly by an altering of the spatial distribution of sound pressure amplitudes in the acoustic far-field through redistribution of energy between the peak of mainlobe, its flanks, and sidelobes. These changes in pdf roughness result in steeper amplitude gradients over direction, which will induce larger changes in spectral signature in the target direction.

The present finding fits well with a number of previous observations that have indicated importance of dynamics in biosonar system of horseshoe bats. Dynamic changes to the shape of the lancet [16], anterior leaf [21], as well as the pinnae [47] have been reported in horseshoe bats. All these dynamic effects were found to occur on time scales that are similar to duration of individual biosonar pulses or echoes. These motions were shown to repeat cyclically from pulse to pulse and have been hypothesized to enhance the encoding of sensory information by individual pulse-echo pairs [47, 21, 16]. In addition, horseshoe bats have been shown to actively adjust their beam width during the terminal stages of prey capture [48].
In this context, the present findings add further evidence to an increasing body of findings in support of the hypothesis that dynamic effects play an important role in encoding of sensory information in the biosonar system of horseshoe bats. The interplay between a conspicuous static feature of the noseleaf shape, the furrows, and a dynamic change (lancet rotation) is particularly noteworthy, because it suggests that the function of the furrows could at least in part be to support dynamic changes to the biosonar beam.

The interplay between static and dynamic features that is suggested by the current findings, could also be relevant in providing bioinspired principles for the engineering of sensory systems. It could serve as an example for how large, controlled changes in emitted wave fields can be brought through dynamic manipulations of devices with static features that could support static as well as dynamic effects.
Chapter 5

Entropy analysis of frequency and shape change in horseshoe bat biosonar

(A part of the work in this chapter is submitted to Journal of Acoustic Society of America (JASA). Reproduced with permission [25].)

This chapter presents the results obtained from the numerical simulations and discusses the variability in sensory information encoded through just the use of frequency or lancet dynamics.

5.1 Abstract

Echolocating bats use ultrasonic pulses to collect information about their environments. Some of this information is encoded at the baffle structures – noseleaves (emission) and pinnae (reception) – that act as interfaces between the bats’ biosonar systems and the external world. The baffle beampatterns encode the direction-dependent sensory information as a function of frequency and hence represent a view of the environment. To generate diverse views of the environment, the bats can vary beampatterns by changes to: 1) the wavelengths
of the pulses or 2) the baffle geometries. Here, we compare the variability in sensory information encoded by just the use of frequency or baffle shape dynamics in horseshoe bats. For this, we use digital and biomimetic prototypes of both noseleaf and pinnae. The beampatterns for all models were either measured or numerically predicted. Entropy was used as a measure to compare the variability in encoded sensory information. It was found that new information was acquired as a result of shape dynamics. Furthermore, the overall variability in the encoded information was similar in case of frequency or shape dynamics. Thus, shape dynamics allows the horseshoe bats to generate diverse views of the environment in the absence of broadband biosonar signals.

5.2 Introduction

Bats have mastered life in complex environments by relying primarily on their biosonar systems to collect sensory information about the presence, location, and nature of sound sources in the environment [49, 11, 50]. A good example of these capabilities are greater horseshoe bats (*Rhinolophous ferrumequinum*), a species that is able to navigate in dense structure-rich vegetation [51, 52] and hunt prey either in flight or by gleaning from surfaces [53, 5]. The sensory information required to accomplish this must be encoded at the interfaces of the bats’ biosonar system and the external world, i.e., as the emitted sounds exit the bat’s nostrils or as the returning echoes impinge on its ears. The space-frequency characteristics of the emission and reception structures can be described by a “beampattern”, a scalar-valued function that specifies the output or input gain of the system as a function of spatial direction and frequency. Each beampattern can hence be seen as a space-frequency filter that provides a certain view of the environment. The ability to generate different beampatterns could help the bats to obtain different views of their environment in order to tailor the received sensory
information to their current needs.

Beampatterns are the result of a diffraction process in which the outgoing or incoming ultrasonic wave packets interact with the surfaces of baffles shapes such as the noseleaves (emission) and the outer ears (reception). Hence, the beampatterns are determined by the geometry of the diffracting surface in conjunction with the wavelength of the diffracted sound. In principle, bats could utilize two different kinds of mechanisms to change their beampatterns, i.e., by virtue of: (i) changing the wavelength of their pulses or (ii) by changing the geometry of the diffracting surfaces. Bat species with broadband ultrasonic pulses (frequency-modulated or FM-bats for short [5]) should be in a good position to vary their beampattern varies as a function of frequency. Their broad frequency bands correspond to a likewise broad range of wavelengths that can interact with the baffle shapes in different ways to generate significantly different beampatterns [54, 55]. In general, beamwidth can be expected to decrease with increasing frequency resulting in a broader view of the environment at lower frequencies and a narrower for high frequencies [56, 57, 58, 17]. In addition to the overall beamwidth, the shape of the beampatterns can depend strongly on frequency in terms of lobes of the beampattern that can appear, disappear, or change position with frequency [59, 17]. Thus, as a result of all these possible variations in the beampatterns with frequency, objects that are located at different angular positions in the environment will get illuminated by different signal spectra that could impact the information that will be encoded in the returning echoes. Echo spectra are known to encode information about the nature and location of targets [5, 58, 59, 60, 61]. As of now, there is very limited evidence that FM bats have control over the shapes that diffract their emitted pulses and the received echoes, an exception being the observation that certain FM bats (Hypsugo bodenheimeri) can change their emission beamwidth by varying their mouth gape [58].

Horseshoe bats (family Rhinolophidae) are so-called CF-FM bats (for constant-frequency
Anupam K. Gupta  Chapter 5. Entropy Analysis of Frequency and Shape Change

- frequency-modulated [11]). Their biosonar calls consist of multi-harmonic signals, where each harmonic is dominated by a long narrow-band portion (CF component) that is framed by a frequency modulated (FM) component at the start and at the end [5].

However, the pulse energy in these calls tends to be concentrated in the CF component with the FM component containing either comparatively low portions of the pulse energy or even being left out completely on occasion [51, 62, 63]. In addition, all but the second harmonic in these multi-harmonic biosonar calls are also relatively weak. This restricts the ability of such bats to generate differing beampatterns due to variation of beam directionality with frequency.

However, unlike what is currently known about FM-bats, CF-FM bats have a very conspicuous dynamic dimension associated with the baffles that surround the sites of ultrasonic emission (noseleaves) and reception (pinna, see Fig.5.1). These baffles can undergo fast non-rigid deformations on time scales similar to the duration of individual pulse emissions and return echoes [16, 21? ]. The deformations are a result of specific muscular action [64, 65] with deformation amplitudes significant in comparison to the wavelength used [16, 21? ].

Some of the recent studies have shown that the deformations of the emission and reception baffles can bring about a significant change in the beampatterns (emission & reception) [16, 17, 24, 22, 66]. In addition, changes in the emission beampatterns of horseshoe bats during natural biosonar behaviors have been recently reported, though the underlying physical mechanism remains unknown [48]. Taken together, these studies suggest that dynamics is an important aspect of bat biosonar. It could be hypothesized that the function of the dynamics in the emission and reception baffle shapes of horseshoe bats is to produce a diversity in the views of the environment that bats with great biosonar bandwidth can achieve by virtue of frequency changes.
The goal of the work presented here has hence been to compare the diversity introduced into views of the environment by the use of either frequency or shape dynamics in horseshoe bats (*Rhinolophous ferrumequinum*) through an information-theoretical (entropy) analysis of the beampatterns. The analyzed beampatterns were obtained from detailed digital models of the natural geometries of noseleaves [17, 24] & pinnae [22] as well as measurements using the biomimetic physical prototypes [24, 67].

Figure 5.1: Different shape sample types used to obtain acoustic far-field (beampattern) data on the noseleaf and pinna dynamics of greater horseshoe bat : a) Portrait of a greater horseshoe bat (BP) b) Digital model used for computer animation of *in-vivo* bat noseleaf dynamics (NN), c) Exact deformable physical replica of the bat noseleaf created through 3D printing (PN, scaled 2× BP) d) Digital pinna model used to recreate bat pinna dynamics (NP), e) Simplified deformable physical prototype of bat pinna (PP, scaled 2.5× BP). Reproduced from [25].
5.3 Methods

5.3.1 Kernel density estimation

It is a non-parametric way to estimate the probability density function (pdf) of a random variable. Unlike the parametric estimators that have a fixed functional form with few parameters that fully define the function, non-parametric estimators like kernel density estimators (KDEs) have no fixed structure and depend upon the sample data points to reach an estimate. The complexity of the fitted KDE model depends upon the sample \([68, 69]\). The larger the sample size, the greater the degree of complexity of the fitted KDE model.

KDE improves over the histograms for pdf estimation by eliminating the two disadvantages that plague histograms: i) roughness, ii) dependence on the bin end points. It does this by placing a smooth kernel at each of the data points. These individual kernels when combined produce a smooth density estimate. However, like histogram dependence on bin-width, KDE depends on the kernel width called as “bandwidth (h)”. Since h controls the complexity of the fitted model, choice of bandwidth is critical to correct estimation of pdf \([68, 69]\).

Multivariate kernel density estimation

Let \(x_1, x_2, \cdots, x_n\) be a sample of \(d\)-dimensional random vectors drawn from a common density function \(f\). The multivariate kernel density estimate is then give by \([70]\):

\[
\hat{f}(x) = \frac{1}{nh^d} \sum_{i=1}^{n} K\left(\frac{1}{h}(x - x_i)\right),
\]

(5.1)

where \(K(x)\) is a multivariate kernel defined for \(d\)-dimensional \(x\) (see eq. 5.2) and \(h\) is the width of the kernel (bandwidth) \([70]\).

\[ \int_{\mathbb{R}^d} K(x)dx = 1, \quad (5.2) \]

The most common used kernel and the one used here is Gaussian kernel (see eq. 5.3) with product kernels – kernels which are products of the kernel function in each dimension – for multivariate density estimation [70].

\[
K\left(\frac{x}{h}\right) = \frac{1}{h\sqrt{2\pi}}e^{\left\{-\frac{x^2}{2h^2}\right\}}, \quad (5.3)
\]

where \( h \) is the kernel width (bandwidth).

The choice of bandwidth \( h \) is critical. If \( h \) is too small, density is a collection of sharp peaks at the data points. If \( h \) is too large, then the KDE estimate is smoothed and details are lost. Hence, a optimal choice of \( h \) is critical to KDE. The choice of \( h \) depends on the data itself, the choice of the kernel and the optimality criterion used for estimation. Several bandwidth estimators have been suggested in literature [71]. In this study we use plug-in type bandwidth estimators [72, 73].

### 5.3.2 Entropy

It is a measure of the uncertainty of a random variable.

**Differential entropy**

For a continuous random variable \( X \) with a probability density function \( f(x) \), Shannon differential entropy is given by [74]:

\[ \text{Shannon differential entropy} = -\int_{\mathbb{R}^d} f(x) \log f(x) dx \]
\[ h(X) = -\int_S f(x) \ln(f(x)) \, dx, \quad (5.4) \]

where \( S \) is the support set of the random variable. The differential entropy depends only on the probability density \( f \) of the random variable (see eq. 5.4).

**Joint differential entropy**

If \( X_1, X_2, \ldots, X_n \) are a set of continuous random variables with joint probability density function \( f(x_1, x_2, \ldots, x_n) \), the joint differential entropy is given by [74]:

\[ h(X_1, X_2, \ldots, X_n) = -\int f(x_1, x_2, \ldots, x_n) \ln(f(x_1, x_2, \ldots, x_n)) \, dx_1 \, dx_2 \cdots dx_n, \quad (5.5) \]

**Nonparametric estimate of differential entropy**

For a non-parametric estimate \( \hat{f}(x) \) of probability density function \( f(x) \) of a continuous random variable using kernel density estimation (KDE), the nonparametric estimate of Shannon differential entropy is given by [75]:

\[ \hat{h}(X) = -\frac{1}{n} \sum_{i=1}^{n} \ln(\hat{f}(X_i)), \quad (5.6) \]

where \( n \) is the number of samples generated from \( \hat{f}(x) \).

Similarly, for a non-parametric estimate \( \hat{f}(x_1, x_2, \ldots, x_n) \) of a joint probability density function \( f(x_1, x_2, \ldots, x_n) \), the nonparametric estimate of joint differential entropy is given by:

\[ \hat{h}(X_1, X_2, \ldots, X_n) = -\frac{1}{n} \sum_{i=1}^{n} \ln(\hat{f}(x_1, x_2, \ldots, x_n)), \quad (5.7) \]
where \( n \) is the number of samples generated from \( \hat{f}(x_1, x_2, \ldots, x_n) \).

### 5.3.3 Quantitative analysis of beampatterns

To obtain the shape data used in present analysis, an adult greater horseshoe (*Rhinolophous ferrumequinum*) bat subject was taken from the caves in the vicinity of Jinan, Shandong Province, China (latitude - 36° 40′ 05″ N, longitude - 116° 59′ 49″ E, elevation - 104′). It was then housed in the lab and noseleaf and pinna motions were recorded using high-speed video cameras. In order to do the acoustic characterization of shape deformations in the study subject, four models that included both digital and physical prototypes of noseleaf and pinna were obtained. The models represented either the exact biological or biomimetic motion.

The life-like digital models were obtained from \( \mu \)CT scans of the noseleaf and pinna samples. In order to recreate baffle dynamics observed in high-speed video recordings of the behaving bat, different set of techniques were used for noseleaf and pinna respectively. For the noseleaf, the digital model was computer-animated using skeletal animation techniques. This involved setting up of a skeleton with control points and joints attached to the mesh such that it approximates observed noseleaf motion in bats [24] (see Figs. 5.1(b), 5.2). For the pinna, a linear elastic finite element model was used to combine the static pinna geometry with the three-dimensional time trajectories of the landmark points (marked on pinna) extracted from video recordings of the behaving bat [22] (see Fig. 5.1(d)). The acoustic properties (beampatterns) of the baffle shape deformations were then numerically predicted [22, 24] (see Fig. 5.3).

Like the digital noseleaf model, the geometry for the physical noseleaf prototype came from \( \mu \)CT scan and was reproduced in full biological detail. The geometry was scaled to twice the size of horseshoe bat noseleaf and fabricated from an elastic material by 3D printing (Objet
3D printer). The geometry was scaled to ease handling and permit use of lower frequencies. The prototype was actuated by a simple linear actuator (Firgelli L12-1) that applied a force from behind to bend the lancet of the noseleaf forward mimicking the motion observed in bats [24] (see Fig. 5.1(c)).

However, unlike the physical noseleaf prototype, the geometry for the physical pinna prototype was a simplified version (scaled 2× the horseshoe bat pinna) of the biological pinna. It was fabricated from an isobutyl rubber sheet and was actuated by a simple linear actuator (Firgelli L12-1) like the noseleaf prototype. A force was applied from the pinna backside to mimic the motion observed in bats [76] (see Fig. 5.1(e)).

The acoustic properties of all four models were characterized by beampatterns that were obtained either by measurement [24, 76] or numerical prediction [22, 24]. These beampatterns were acquired over a range of angles that spanned 180° in azimuth and 120° in elevation with a resolution 3°. For all models, the beampatterns were obtained for five equidistant frequencies across bats’ biosonar frequency broadcast range (60-80 kHz). The frequencies were adjusted inversely to compensate for scaled physical models respectively.

To compare the variability in the sensory information encoded across frequency and shape change (diversity of views), the beampatterns were characterized by kernel density estimates (KDE) [70] of the probability density functions (pdfs) of the beampattern amplitudes. To compute the KDE estimates of the amplitude pdfs, a gaussian kernel was used. The size (bandwidth) of the kernel was selected automatically using a plug-in type estimator [70, 72, 73]. The amplitude pdfs computed by KDE to characterize the beampattern data are as follows:

1. Two-dimensional joint amplitude pdfs combining beampatterns associated with different frequencies. One dimension of these pdfs was the beampattern amplitude at
a reference frequency of 60 kHz and the other the beampattern amplitude at one of
the five frequencies at which the bat’s main biosonar band (60-80 kHz) was sampled.
The values of the pdf were estimated for 2501 points along each dimension. Joint
pdf estimates were obtained for each of the shape conformation stages in the studied
sample.

2. Two-dimensional joint amplitude pdfs combining beampatterns associated with differ-
ent shape conformation stages (see Fig. 5.4). One dimension of these pdfs was the
beampattern amplitude associated with the upright shape change stage and the other
the beampattern amplitude associated with one of the five stages in the entire shape
change cycle. The values of the pdf were estimated for 2501 points along each dimen-
sion. Joint pdf estimates were obtained for each of the frequencies analyzed.

3. Five-dimensional joint amplitude pdfs where each dimension represented the beampat-
tern amplitude for one of the five shape change stages in shape change cycle. Along each
dimension the pdf values were estimated for 2501 points. A separate five-dimensional
joint pdf was computed for each of the analyzed frequencies.

4. Five-dimensional joint amplitude pdfs where each dimension represented one of the five
equidistant frequencies in the bat’s biosonar range (60-80 kHz). Along each dimension
the pdf values were estimated for 2501 points. A separate five-dimensional joint pdf
was computed for each of the stages in the shape change cycle represented in the
sample.

For each of the above kernel density estimate (KDE) of amplitude pdfs, differential en-
tropy [75, 73] (see Eq. 5.8) was computed to quantify the differences in variability in the
sensory information encoded by just the use of frequency and shape change respectively.

\[
\hat{H}(f) = -\frac{1}{n} \sum_{i=1}^{n} \ln(\hat{f}(X_i))
\]  

(5.8)

where \(\hat{H}(f)\) is the nonparametric estimate of differential entropy \(H(f)\), \(\hat{f}\) is the kernel density estimate (KDE) estimate of probability density function (pdf) and \(n\) is the no of samples.

### 5.4 Results

The joint 2D probability density functions of the normalized beampattern amplitudes across shape change stages (Fig. 5.4) and across frequency (Fig. 5.5) were both found to have intricate patterns, i.e., the beampattern amplitudes across different frequencies or shape conformations were found to have complex statistical dependencies, evident in multiple ridges in the pdfs. The patterns in the joint 2d pdfs differed between the shape conformations and the frequencies indicating that the statistical dependencies are not the same for changes in shape and changes in frequency.

For changes in baffle shape, the joint entropy values estimated from the joint pdfs depended on the distance between the two shape conformations that were used to compute the joint entropy (Fig. 5.6(a)). The further a tested conformation stage was separated from the upright stage that was used as a reference, the larger the joint entropy between these two stages. With the exception of the numerical noseleaf model (NN), an average increase of one bit (approx. 21%) in joint entropy between the first and last deformation stages was observed across all models (Fig. 5.6(a)).

The joint entropy values computed by combining different frequencies did not show the same systematic dependence on distance between the compared beampatterns that was seen among
Figure 5.2: Digital rigged noseleaf model of greater horseshoe bat (Rhinolophus ferrumequinum): a) front view, b) side view, c) Lancet anterior-posterior motion recreated in digital bat noseleaf model using skeletal animation techniques (rigging). Reproduced from [25].
Figure 5.3: Numerically predicted beampatterns for bat noseleaf digital model. Each row shows different lancet positions. Each column shows different frequencies. The grey-level coding is linear. Reproduced from [25].
Figure 5.4: Joint probability density function across lancet shape change. The rows show the 2D joint probability density functions between the lancet upright stage (LR - 0°) and subsequent shape change stages i.e. LR - 2° & LR - 6° respectively, in the shape change cycle. The columns show the joint pdfs between lancet shape change stages for multiple frequencies in bats’ biosonar frequency broadcast range (60-80 kHz).Datasets used here are numerically predicted acoustic estimates for NN model. NN refers to the sample shown in Fig.1. LR refers to lancet rotation. Reproduced from [25].
Figure 5.5: Joint probability density function across frequency. The rows show the 2D joint probability density functions between the lowest frequency (60 kHz) and subsequent frequencies i.e. 65 kHz & 75 kHz respectively in bats’ biosonar frequency broadcast range (60-80 kHz). The columns show the 2D joint pdfs between frequencies for multiple lancet shape change stages in the shape change cycle. Datasets used here are numerically predicted acoustic estimates for NN model. NN refers to the sample shown in Fig.1. LR refers to lancet rotation. Reproduced from [25].
Figure 5.6: Average joint entropy estimates in bits. (a) From left to right, bar height represents the joint entropy estimate for a shape change stage with upright (reference) stage as a function of distance from the upright (reference) stage in shape change cycle (averaged over five equidistant frequencies between 60-80 kHz). (b) From left to right, bar height represents a joint entropy estimate for a frequency with lowest frequency (60 kHz) as a function of distance from the lowest frequency in bats’ biosonar frequency broadcast range (60-80 kHz) divided into five equidistant frequencies (averaged over five stages in shape change cycle). Error bars indicate the minimum and maximum values of entropy. NN, PN, NP, PP refer to the samples shown in Fig.1. Reproduced from [25].
Figure 5.7: Pooled average entropy estimates in bits. Light gray bar height represents the joint entropy estimate across all the shape change stages (averaged over five equidistant frequencies between 60-80 kHz). Dark gray bar height represents the joint entropy estimate across all five equidistant frequency in bats’ biosonar frequency broadcast range (60-80 kHz) (averaged over five stages in shape change cycle). Error bars indicate the minimum and maximum values of entropy. NN, PN, NP, PP refer to the samples shown in Fig.1. Reproduced from [25].
the changes in shape. For the frequencies, a reference frequency of 60 kHz was compared to five frequencies spaced equally between 60 and 80 kHz. For all models, this comparison let to an average joint entropy change of 0.4 bits (approx. 12%) between the lowest and highest entropy values regardless of the spectral separation between the two frequencies (Fig. 5.6(b)).

To compare the variability in encoded information across all five shape conformation stages and five frequencies, five dimensional joint pdfs were estimated for both cases, i.e., across frequency and shape change. The entropy estimates for the joint pdfs across all five shape change stages and five frequencies were found to be comparable, with an average difference in entropy of 1.2 bits (approx. 8%) observed across all models (Fig. 5.7).

5.5 Discussion

In the results presented here, both shape change and frequency change were found to have an approximately equal effect on increasing the variability (entropy) of the sensory inputs. The only difference found between the two approaches to altering the beampattern was that whereas the differential entropy values increased with the distance between different shape conformations, they remained approximately the same between frequencies, i.e., regardless of the spectral distance between these frequencies. Since the change in wavelengths (about 1.5 millimeter over the analyzed frequency band) were substantially less than the maximum displacements associated with the changes in shape (several millimeters), this cannot be explained by the amplitude of the geometrical changes. Instead, it could be hypothesized that the difference is due to the local nature of the shape changes where only certain parts of the baffle being moved versus the global nature of the frequency changes where the wavelength changes affect the entire diffraction process.

The observed similarity between the variability that has been introduced by changes in baffle
shapes or frequency changes indicates that both types of changes could be equally well suited for enhancing the encoding of sensory information through the diverse sets of beampatterns they create. Hence, horseshoe bats could have two alternative mechanisms for increasing the amount of sensory information they receive via their biosonar echoes: relying on the echoes to the FM-tails of their biosonar pulses or changing the shape of their noseleaves and pinnae. The bats could use both mechanisms for pulses that contain strong FM-tails and are accompanied by noseleaf and/or pinna motions. They could rely on frequency diversity only for pulses that have strong FM-tails but are not accompanied by any dynamic shape changes. Finally, the bats could rely on shape diversity only in situations where the FM-tails are weak, but the CF-components of their pulses are accompanied by dynamic changes in baffle shape. Only in cases, where the bats emit pulses with a weak FM-tail and no shape changes would they be left with a minimum of monaural information related to target direction.

The need to concentrate pulse energy in a narrow frequency band for the detection of Doppler shifts could have been an evolutionary driving force behind the evolution of the noseleaf and pinna dynamics in horseshoe bats. The narrower the frequency band of the pulses, the smaller the amount of monaural, direction-related sensory information that the animals have access to. Noseleaf and pinna deformation could hence be seen as evolutionary innovations to break this linkage between bandwidth and the encoding of monaural direction information. The current findings affirms the importance of biosonar dynamics in the biosonar system of horseshoe bats which is in accordance with a host of recent studies: Dynamic changes in the shape of lancet [16], anterior leaf [21] and pinnae [22] have been previously reported. These motions were found to occur on timescales of individual pulses or echoes and have been hypothesized to have an effect on encoding of sensory information [16, 21, 22]. Moreover, horseshoe bats have been shown to actively adjust beam width during terminal stages of prey
The present findings give further credence to the hypothesis that dynamics plays an important role in the encoding of sensory information. The current finding is particularly interesting as it suggests that baffle shape change could be a novel way evolved by CF-FM bats to generate diverse beampatterns to tailor the biosonar view to the task at hand in the absence of broadband biosonar signals.
Chapter 6

A dynamic substrate for the physical encoding of sensory information in bat biosonar

(This chapter is submitted in Physics Review Letters (PRL) and is currently under review. Reproduced with permission [23].)

This chapter discusses the performance improvements achieved in localization performance of horseshoe bat biosonar performance due to shape dynamics using an information-theoretic based analysis of data.

6.1 Abstract

Horseshoe bats have dynamic biosonar systems with interfaces for ultrasonic emission/reception that change shape while diffracting the outgoing/incoming sound waves. An information-theoretic analysis based on numerical and physical prototypes shows that these shape changes add sensory information (mutual information between distant shape conformations < 20%), increase the number of resolvable directions of sound incidence, and improve the accuracy of direction finding. These results demonstrate that horseshoe bats have a highly effective
substrate for dynamic encoding of sensory information.

6.2 Introduction

Like many hearing systems in biology, bat biosonar encodes information about the presence [77], location [78], and characteristics of sound sources [79, 80] in the environment [11]. However, unlike many of its peers, bat biosonar by itself has the proven capability of encoding sensory information sufficient for rapid navigation in three dimensions, often in highly complicated environments [81]. The sites of ultrasound emission and reception are critical for the encoding of this information, because they are the only system stages at which direction-dependent acoustic diffraction can take place [19]. Hence they provide the sole physical substrate for the encoding of sensory information related to target direction. Probably because of this pivotal functional position, many bat species have evolved elaborate baffle shapes that diffract their ultrasonic pulses upon emission (noseleaves, in species with nasal emission) as well as during reception (pinnae). In horseshoe bats (family Rhinolophidae, [82]), shape features of the noseleaves [83] and the pinnae [66] have been linked to the distribution of the emitted energy and the receiver sensitivity as a function of direction (beampatterns). Over the recent years, a growing body of evidence has accumulated to suggest that, beyond their static geometric complexity, the noseleaves and pinnae of horseshoe bats have a prominent dynamic dimension [84]. Fast dynamic shape changes that go beyond rotations of static shapes [40, 85] have been demonstrated to occur in both interface structures, noseleaves [16, 21] and pinnae [22, 65]. Along with the dynamic changes to the interface shapes, changes to the emission beampatterns during natural biosonar behaviors have been reported, but the underlying acoustic mechanisms remain unclear [48]. Evidence from several sources supports the hypothesis that the shape changes in the biosonar interfaces
play a functional role: (i) the shape changes are effected by elaborate muscular actuation mechanisms [64, 65], (ii) bats control the dynamic shape configuration sequences based on behavioral context [21, 65], (iii) shape deformations coincide with ultrasonic diffraction in time [16, 21], (iv) the magnitudes of the shape changes are significant compared to the transmitted wavelength [16, 21, 22]. In accordance with (iv), noseleaf and pinna deformations in horseshoe bats have been predicted to produce qualitative changes in the beampatterns [16, 22, 17]. Similar changes have been demonstrated experimentally with biomimetic reproductions of horseshoe bat noseleaves [86] and pinnae [66, 24]. In these experiments, the shape deformations have been found to result in time-variant device characteristics [86, 87]. In the frequency domain, the beampatterns typically alternated between patterns where all sensitivity was concentrated in the direction of a single mainlobe and others where sensitivity was scattered more widely among local maxima (sidelobes) [22, 66].

Investigating the impact of these dynamic effects on the encoding capacity for sensory information requires four-dimensional characterizations, i.e., emission amplitudes or sensitivity gains measured over time, two direction angles, and frequency [87]. Data of sufficient quantity and quality for such characterizations is very difficult to obtain from live bats – even under laboratory conditions. Therefore, the present work has been based on two types of datasets: numerical beampattern estimates derived from detailed digital models of the natural geometries of the noseleaves and pinnae [22, 24] and beampattern measurements taken from biomimetic physical prototypes (either with full details or simplified) [67, 76]. The numerical and physical experiments resulted in four different datasets (see Figure 6.1) that were used as a basis for an information-theoretic analysis of the dynamics in horseshoe bat biosonar system.
6.3 Methods

6.3.1 Datasets

Adult greater horseshoe bats (*Rhinolophus ferrumequinum*) served as study subjects for the recording of the non-rigid noseleaf and pinna motions. The animals were taken from caves in the vicinity of the city of Jinan in western Shandong Province, China. They were housed in an indoor facility for a few days prior to the motion capture experiments [16, 21, 22]. During their time in captivity, they were fed on the diet of mealworms (*Tenebrio molitor*). Water was provided ad libitum.

Based on the qualitative and quantitative analysis of the shape deformations observed in the study subjects, four different datasets were obtained that represented biological as well as biomimetic deformations (see Fig. 6.1). The models were either physical prototypes or numerical simulations. In particular, the following four models were created:

![Figure 6.1: Different sample types used to obtain acoustic far-field (beampattern) data on the emitter and receiver dynamics of greater horseshoe bat biosonar: NN) Digital noseleaf model used for computer animation of *in-vivo* dynamics followed by numerical analysis, PN) Detailed physical replica of the noseleaf created through additive manufacturing (scaled 2×), BP) Portrait of a greater horseshoe bat, NP) Digital pinna model used to recreate dynamic behavior of 3d landmarks obtained from stereo high-speed recordings, PP) Simplified deformable physical prototype modeled after the horseshoe bat pinna (scaled 2.5×). Reproduced from [23].](image-url)
i) a digital noseleaf model that was based on the static geometry of a post-mortem sample that was obtained by virtue of a \( \mu \)CT scan. The noseleaf geometry was computer-animated (skeletal animation approach) to approximate the shape dynamics seen in high-speed video recordings of live horseshoe bats [24]. The shapes of the animated digital model were analyzed numerically to predict the time-variant acoustic device characteristics.

ii) a physical noseleaf prototype was fabricated from an elastic material with an additive manufacturing technique (Objet 3D). As for the digital model, the geometry of the physical model came from a \( \mu \)CT scan. Hence, the physical noseleaf model replicated life-like geometrical detail. For the ease of handling and to allow the use of lower frequencies for the device characterization, the prototype was scaled to \( 2 \times \) the size of the horseshoe bat noseleaf. The prototype was actuated in a simple fashion with a linear actuator (Firgelli L12-1) that was used to bend the lancet of the noseleaf forward [24] as has been observed in horseshoe bats [16].

iii) a life-like digital pinna model was created by combining a complete digital pinna geometry with a set of three-dimensional time trajectories of landmark points. The complete geometry was reconstructed from \( \mu \)CT scans of the pinna and the time trajectories were obtained from stereo high-speed video recordings of the pinna of a behaving bat on which landmark points had been painted [22]. The static pinna geometry and the time trajectories were combined by a finite element model of a linearly elastic material that was used to interpolate the landmark points with the pinna geometry. The acoustic properties of the deformed pinna shapes were predicted using numerical methods.

iv) a simplified physical model of a deforming pinna was fabricated from a sheet of isobutyl rubber [66, 76]. The rubber sheet was cut into shape and rolled up to form an obliquely truncated cone. The cone was then augmented with three biomimetic local shape features: a vertical ridge, an incision on the rim, and a frontal flap that mimicked the prominent
antitragus of the horseshoe bats. The size of the entire prototype and its local shape features were scaled by a factor of 2.5 in order to allow the use of lower frequencies for the acoustic device characterization. Biomimetic shape changes were implemented with a single linear actuator that bent the biomimetic pinna by inserting a force on the backside of the pinna [66]. The biomimetic bending pattern of the baffle resulted from the asymmetry in the force insertion and the baffle (including local features).

The acoustic characteristics of all models were determined in the form of beampatterns that were either measured or predicted numerically. All the measurements or estimates were obtained over a range of angles that spanned 120° in elevation and 180° in azimuth with a resolution of 3°. For each model, the beampatterns were obtained for five equidistant frequencies between 60 and 80 kHz. For the physical models, the frequencies used in the measurements were inversely scaled to compensate for the scaling of each of the physical models.

### 6.3.2 Quantitative analysis of beampatterns

**Direction resolution**

The impact of the beampattern dynamics on the encoding of information regarding the direction of a target was quantified by virtue of the differential entropy (see Fig. 5.6) between the actual target direction and the biosonar’s direction estimate with a method developed by Buck [88]. Because the computed measure is an upper bound on the mutual information, it provides the best possible directional resolution in the form of the maximum number of resolvable directions. The approach does not provide any insights into how this maximum number of resolvable directions could be achieved through a specific partition of the direction space. Direction estimation is modeled as a communication task where each target –
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inadvertently — communicates its direction through a spectral signature that is introduced by the direction-dependent diffraction at the noseleaf or pinna. The direction-dependent spectral signatures that can be used for the direction estimates are corrupted by additive noise. Here, it was assumed that the spectral amplitude values and the additive noise both have Gaussian probability density functions. This assumption results in an upper bound for the mutual information, because the Gaussian probability density functions maximize the differential entropy for a given covariance. Under this assumption, the upper bound on channel capacity \( C \) (in bits) can be computed as

\[
C \leq I_{\text{max}}(X, Y) = \frac{1}{2} \log_2 \frac{|K_{YY}|}{|K_{NN}|},
\]

(6.1)

where \( X \) is the vector formed by the normalized spectral magnitudes obtained for five equidistant frequencies and \( Y \) is the vector of noisy observations of these magnitude values, i.e., \( Y = X + N \) where \( N \) is a vector of samples drawn from an i.i.d. zero-mean Gaussian random process with variance \( \sigma_N^2 \). The matrices \( K_{YY} \) and \( K_{NN} = \sigma_N^2 I \) are the covariance matrices of the observations and the additive noise respectively. The covariance matrices are given by

\[
K_{XX} = E(XX^T) - E(X)E(X^T).
\]

(6.2)

The expression for the upper bound (Eq. 6.1) uses the determinants of these covariance matrices (denoted by \(|\cdot|\)). The directional resolution was also expressed as the maximum number of distinguishable directions given by \( 2^C \). Channel capacity estimates were obtained for a range of signal-to-noise ratios (SNR) given by

\[
\text{SNR} = 10 \log_{10} \frac{\text{trace}(K_{XX_{avg}})}{\text{trace}(K_{ZZ})},
\]

(6.3)
where $K_{XX_{avg}}$ is the average of the covariance matrix taken across all sensor conformation stages.

**Direction Estimation accuracy**

As an alternative way to quantify the impact of the dynamically encoded information on direction estimation, the Cramér-Rao lower bound (CRLB) [89], a measure of local estimation accuracy, was computed for all four datasets. The CRLB gives the minimum variance of the direction estimates that is possible for any estimator. Here, the CRLB calculations were based on the assumption that direction estimation is based on observations of the signal amplitudes across the five frequency channels represented in the current data sets. As was the case for the direction resolution, an additive white Gaussian noise model was used and the noise was assumed to be independently and identically distributed over frequency as well as direction. Under these assumptions, the Fisher information matrix ($I_{Fisher}$) for the joint estimation of azimuth ($\phi$) and elevation ($\theta$) was then computed as [20]:

$$I_{Fisher}(\theta, \phi) = \text{SNR} \left[ \sum_{f=1}^{5} \left[ \frac{\partial D_f(\theta, \phi)}{\partial \theta} \right]^2 - \sum_{f=1}^{5} \frac{\partial D_f(\theta, \phi)}{\partial \theta} \frac{\partial D_f(\theta, \phi)}{\partial \phi} \sum_{f=1}^{5} \left[ \frac{\partial D_f(\theta, \phi)}{\partial \phi} \right]^2 \right], \quad (6.4)$$

where $D_f(\theta, \phi)$ is the measured or computed beampattern gain at the $f^{th}$ frequency.

The spatial derivatives in Eq. 6.4 were estimated from the numerical predictions or measurements of the beampattern functions using a two-dimensional “derivative of Gaussian” filter with a width (standard deviation) of $9^\circ$. In all datasets, the beampattern functions ($D_f(\theta, \phi)$) themselves were sampled with a $3^\circ$ resolution for in azimuth and elevation. The CRLB is obtained as the inverse of the Fisher information matrix. For the direction-finding problem considered here, the CRLB is a $2 \times 2$ covariance matrix where the two diagonal
elements give the lower bounds on the variance of the estimates in azimuth and elevation respectively and the off-diagonal elements are the covariances between the estimates. The CRLB covariance matrix was decomposed into its eigenvectors and eigenvalues to find the principal directions of the error and the variance along these directions. The eigenvector associated with the larger eigenvalue represents the axis along which the largest variability in the direction estimates occurs. The eigenvector associated with the smaller eigenvalue corresponds to the axis of least variability of the estimates. Hence, the eigenvectors and eigenvalues can be used to the major and minor axes of an error ellipse. This was done for each direction on the azimuth-elevation grid of the data set. Based on the assumption of a Gaussian error distribution, the size of the error ellipses was scaled so that they represent a 90% confidence interval for the estimates.

6.4 Results

In order to assess whether the additional information gained by virtue of the sensor dynamics has a concrete impact on biosonar performance, an upper bound on resolving different directions that is based on the concept of Gaussian channel capacity [88] was computed over a range of lower signal-to-noise ratios (SNR≤20 dB). This upper bound can be seen as a global measure of resolution because it gives a maximum total number of directions that can be resolved over the entire direction domain without specifying a partitioning for this domain that would be suitable for achieving the maximum number of resolved directions. As expected, the maximum number of resolvable directions increased with SNR for all samples and conformation stages (see Fig. 6.2). Repeated measurements based on the same device conformation stage resulted in a resolution improvement that is predicted by the effect of averaging five independent samples on the SNR (≈ 7 dB). Combining sensory information
across different conformation stages resulted in a resolution improvement that went significantly beyond the effect of averaging over repeated measurements taken with the same device conformation. As the SNR increased, the gap between the resolutions provided by averaging and those achieved by integration across different conformation stages widened. At an SNR of 6 dB, for example, single measurements from single device conformations provided for a direction resolution of 3.7 bits (i.e., \(\sim 13\) different directions) on average. Averaging over five measurements from identical conformations improved the upper bound on the resolution to 7.5 bits (i.e., \(\sim 181\) resolvable directions) and combining measurements across five different conformations added another 3.5 bits, bringing the total number of resolvable directions to \(\sim 1,867\). At a higher SNR of 12 dB, integrating different instead of identical conformations added 9.5 bits of resolution, increasing the upper bound on the number of resolvable directions from 3,100 to 2.2 million.

As a second way to evaluate the impact of the increased sensory encoding capacity on sensory estimation performance, the local accuracy of direction finding was measured by the Cramér-Rao lower bound (CLRB, \([89]\)) at higher SNRs (e.g., 40 dB, Fig. 6.3). As was the case for the upper bound on direction resolution, the performance bound was significantly improved when information collected across different conformation stages was combined. The larger values in the distribution of errors, in particular, were greatly reduced by incorporating different conformation stages (Fig. 6.3). In all four data sets, the average of the maximum value for the lower bound on the standard deviation of the estimate, i.e., the length of the major axis of the error ellipse, was reduced from 22 to 13.5° when different conformations instead of a single repeated conformation were used (see Fig. 6.3).
Figure 6.2: Combining stages of a dynamic sensor increases the directional resolution in the presence of noise. Directional resolution is quantified by an upper bound on the number of resolvable directions that is a function of signal-to-noise ratio (additive white Gaussian noise). The upper bound is expressed either directly as the maximum number of resolvable directions (right-hand axis) or as a directional resolution (in bits, i.e., \( \log_2 \) of the maximum number of resolvable directions, left-hand axis). Blue: individual sensor conformation stages, green: effect of averaging signals from an identical sensor conformation stage five times, red: effect of combining five different sensor conformation stages. NN, PN, NP, PP refer to the samples as shown in Fig. 6.1. Reproduced from [23].
Figure 6.3: Combining dynamic sensor conformations increases directional accuracy. Estimation accuracy quantified by Cramér-Rao lower bound (CRLB). Top row: map of error ellipses (90% confidence intervals) for repeated individual sensor conformation stage (left-hand side) and combination of five different sensor conformation stages (right-hand side). Error ellipses are drawn on top of the averages over all beampatterns gains used in the respective scenario. Bottom row: distribution of accuracy (major axis of the error ellipses). Blue: individual sensor conformation stages, green: effect of averaging the same stage five times, red: effect of using five different sensor conformation stages. NN, PN, NP, PP refer to the samples as shown in Fig. 6.1. Reproduced from [23].
6.5 Discussion

The results of the present study demonstrate that the dynamic conformation changes of the noseleaves and pinna seen in horseshoe bats significantly increase the coding capacity for sensory information. This result was obtained using a discretized version of the continuous device conformation sequence seen in nature. It remains to be determined what the coding capacity of the entire continuous conformation sequence would be, but the fast decay of mutual information with distance between the discrete conformation stages seems to suggest that the joint entropy over the entire continuous sequence could be several times that of an individual conformation stage. Furthermore, the results presented here demonstrate that this additional coding capacity can be used to improve performance in standard sonar estimation tasks related to source-direction finding.

It is noteworthy that the observed effects on information capacity and estimator performance were qualitatively and quantitatively similar across four very different data sets. The presence of the coding-capacity effects in data obtained from numerical predictions as well as from physical measurements renders it unlikely that these results were due to some methodological artifact, since the two methods used had little in common. The presence of the effects in detailed reproductions of biological shape geometry and dynamics as well as in simplified biomimetic models suggests that the effects are highly robust. This argues against an artifact or any other type of irreproducible result that depends on details of the particular sample that are unlikely to be seen in any other realization. The apparent robustness of the effects is also particularly important for potential engineering applications, because it makes it likely that these effects can be harnessed even under circumstances that force deviations from the original biological paragons.

In the present work, the utility of the dynamic effects has been demonstrated in the context
of traditional sonar sensing tasks, namely direction resolution and accuracy. While these tasks can be expected to be of pivotal importance to any (bio)sonar system, they may not be sufficient to explain how biosonar meets the bats’ sensory information needs. Hence, it remains an open question if the dynamics of horseshoe bat biosonar could also explain some of the animals’ most astounding sensory capabilities that have yet to be reproduced by engineered systems. Examples of the latter are the abilities of bats to navigate in dense natural environment or to fly and hunt in dense swarms. Since the dynamic effects analyzed here add an additional temporal dimension to the sensors, they could provide novel ways to address the challenges associated with these and related sensing tasks. If this is the case, bioinspired dynamic principles could allow man-made sensor technology to master the same challenges and hence close the performance gap between active sensing in biology and in engineering.
Chapter 7

Summary

This chapter summarizes the work performed for this dissertation and presents suggestions for the future work.

7.1 Major findings

The following major findings have resulted from the work presented in this dissertation:

1. The dynamic changes in lancet, a triangular flap at the posterior of the horseshoe bat noseleaf, significantly altered the spatial distribution of sound pressure amplitudes in the far-field through redistribution of energy between the peak of mainlobe, its flanks, and sidelobes. These changes were a property of the entire frequency band but were highly variable from frequency to frequency [17].

The effects of dynamic changes of the lancet on the spatial distribution of sound pressure amplitudes disappeared in the absence of furrows. This can be taken as an evidence for an interaction between the acoustic diffraction effects of the static local
shape feature – furrows– and lancet dynamics [17].

2. New sensory information can be encoded through dynamic shape changes in the lancet. The joint entropy decreased on average by approx. 21% between consecutive stages in shape change cycle [25]. This can be taken as evidence for our hypothesis of functional significance of deformable structures in bat’s coding capacity.

3. The variability in the encoded sensory information by just the frequency or dynamic shape changes in the lancet were similar. The joint entropy between the two approaches differed by only approx. 8% [25]. This supports our hypothesis that use of shape dynamics could be a novel way evolved by CF-FM bats to generate diverse beampatterns to tailor the biosonar view to the task at hand in the absence of broadband biosonar signals.

4. The biosonar performance improved significantly by encoding of additional sensory information through dynamic shape changes. This can be taken as further evidence supporting our hypothesis of significance of deformable structures in bat’s sensory information coding capacity. The upper bound on maximum number of resolvable directions increased by an order of magnitude over just the effect of averaging at a SNR of 6 dB. The gap widened further with an increase in SNR. Similarly, the local target direction estimation accuracy improved with dynamic shape changes. In the studied datasets, the maximum value for the lower bound on the standard deviation of the estimate, i.e., the length of the major axis of the error ellipse, was reduced by at least 20% on average when different conformations instead of a single repeated conformation were used.
7.2 Discussion

We have shown here that noseleaf dynamics helps bats to control the spread of the emission beam. This is done through a spatial redistribution of energy in mainlobe, flanks and sidelobes. This allows bats to generate diverse beampatterns – from single lobe beampatterns to beampatterns with multiple lobes – to obtain diverse views of the environment. Furthermore, the variability in sensory information encoded through the use of dynamics was found to be similar to information encoded through the use of frequency change. This suggests that shape changes could be a novel way evolved by CF-FM bats to generate diverse beampatterns to tailor the biosonar view to the task at hand in the absence of broadband biosonar signals.

The dynamic shape changes in horseshoe bat noseleaf and pinna allows horseshoe bats to encode new sensory information about the environment. This additional sensory information as demonstrated here, improves the performance of biosonar system on two traditional sonar sensing tasks – direction resolution and accuracy of direction finding – significantly.

The above findings confirm that biosonar dynamics plays an important role in the bat biosonar system. However, it is still unknown how biosonar meets the bats’ sensory needs to navigate in complex natural environments. This leaves a possibility that dynamics could be a key factor behind astounding sensory capabilities of bats when negotiating complex environments like navigating in dense vegetation or flying and hunting in dense swarms. The current engineering systems pale in performance to bats in such environments. Since the dynamic effects analyzed here add an additional temporal dimension to the sensor, they can provide novel ways to improve man-made sensory systems to master the same challenges and help close the performance gap between active sensing in biology and in engineering.
7.3 Suggestions for future work

1. This study can be extended to include more bat families like *Hipposideridae* that have dynamics associated with baffle structures – noseleaves & pinnae – to investigate if the effects produced by dynamic shape changes are similar in nature.

2. The impact of dynamics shapes changes on performance of bats in high level tasks like target classification, navigation & prey hunting can be investigated.

3. The mechanism by which the changes produced by dynamics are interpreted in the bat auditory system beyond pinnae (outer ears) and their influence on decision making process can be investigated.

4. A comparative study of performance of bats with & without dynamics on similar tasks can be undertaken.

5. A study to investigate the relationship between particular perceptual problem that bats face in a particular surrounding and presence of dynamics can be undertaken.
Bibliography


Appendix A

Beampatterns: Chapter 4

Additional beampattern data used for results presented in chapter 4.
Figure A.1: Numerically predicted beampatterns for bat noseleaf model 2. Each row shows different lancet positions & corresponding furrow configuration. Each column shows different frequencies. The gray level coding of amplitudes is logarithmic and the level of mainlobe contour line is at -3dB.
Figure A.2: Numerically predicted beampatterns for bat noseleaf model 3. Each row shows different lancet positions & corresponding furrow configuration. Each column shows different frequencies. The gray level coding of amplitudes is logarithmic and the level of mainlobe contour line is at -3dB.
Appendix B

Beampatterns: Chapter 5 & 6

Addition beampattern data used for results presented in chapter 5 & 6.

Figure B.1: Numerically predicted beampatterns for bat pinna digital model. Each row shows different pinna positions. Each column shows different frequencies. The grey-level coding is linear.
Figure B.2: Numerically predicted beampatterns for bat noseleaf physical prototype. Each row shows different lancet positions. Each column shows different frequencies. The grey-level coding is linear.
Figure B.3: Numerically predicted beampatterns for bat pinna physical prototype. Each row shows different pinna positions. Each column shows different frequencies. The grey-level coding is linear.