

## Dynamics of biosonar systems in Horseshoe bats

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**Abstract.** Horseshoe bats have an active ultrasonic sonar system that allows the animals to navigate and hunt prey in structure-rich natural environments. The physical components of this biosonar system contain an unusual dynamics that could play a key role in achieving the animals' superior sensory performance. Horseshoe bat biosonar employs elaborate baffle shapes to diffract the outgoing and incoming ultrasonic wave packets; ultrasound is radiated from nostrils that are surrounded by noseleaves and received by large outer ears. Noseleaves and pinnae can be actuated while ultrasonic diffraction takes place. On the emission side, two noseleaf parts, the anterior leaf and the sella, have been shown to be in motion in synchrony with sound emission. On the reception side, the pinnae have been shown to change their shapes by up to 20% of their total length within  $\sim 100$  milliseconds. Due to these shape changes, diffraction of the incoming and outgoing waves is turned into a dynamic physical process. The dynamics of the diffraction process results in likewise dynamic device characteristics. If this additional dynamic dimension was found to enhance the encoding of sensory information substantially, horseshoe bat biosonar could be a model for the use of dynamic physical processes in sensing technology.

Dynamic principles are well known to play important roles in biological function. This is immediately obvious for functions that are directly linked to physical motions such as growth (e.g., cell migration [34], locomotion ([9, 17], and interactions between mobile individuals, e.g., in the form of animal swarms or other collective behaviors [7]. However, dynamic principles could be even more pervasive and extend into functions such as sensing, where a role for dynamic principles may not be immediately obvious. There is a growing body of evidence that the biosonar of certain bat species could represent a case where dynamic effects are an integral part of a biological sensory system. The goal of this review is to present what is currently known about dynamic effects in bat biosonar. The research to be reviewed here is based on work with animals as well as with biomimetic systems. The findings that have been obtained so far will be discussed in the context of sensory information encoding and parallels will be

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drawn between biosonar and comparable engineered sensory systems such as sonar and radar. The purpose of this review is to serve readers who are looking for a concise summary of the dynamics in bat biosonar and how it may fit in with sensory encoding in the physical domain.

## 1 Bat biosonar & its technical peers

Bats (order Chiroptera) are a group of mammals that has achieved a remarkable evolutionary success. There are more than 1,200 known bat species [68], a number that amounts to about 20% of all mammalian species and makes bats the second most species-rich order of mammals after rodents (order Rodentia). Furthermore, bats have settled the entire land surface of the earth – with the exceptions of the polar icecaps and a few remote oceanic islands. Bats can be locally and regionally abundant, and some species form large colonies that can reach many millions of individuals in size [1,26].

The most conspicuous feature that sets bats apart from all other mammals is a combination of powered flight and sonar. It has been hypothesized that this unique combination has been a key factor behind evolutionary success of bats [69]. This judgment is based on the observation that the flapping flight and sonar sensing of bats are both highly capable systems that have enabled bats to be exceptionally successful in a variety of ecological niches. Bat flight is based on flapping wings with an unmatched amount of flexibility. Not only do bats have the degrees of freedom afforded by the joints in their hand skeleton to control their wings, they also have muscles in the wing membranes that are active during flight [12]. This flexibility has given bats a high degree of maneuverability, efficiency [75], as well as load-carrying capacity.

The bats' biosonar system is likewise notable for its capabilities. While all bat species have some visual abilities, biosonar is a sufficient, primary far sense for many species [52]. Bats use both active and passive sonar. When using active biosonar, the bats analyze echo returns triggered by their own ultrasonic emissions. When using passive sonar, the bats are listening to sounds from a foreign source. An prime example for the passive approach is the fringe-lipped bat (*Trachops cirrhosus*), a frog-eating species, that uses its prey's mating calls for detection [61]. However, even this bat species still uses active sonar along with the passive sonar when hunting its prey [5].

Over the course of about 50 million years of evolution [69], bats and their biosonar systems have undergone a diversification (“adaptive radiation”) that has led to the exploitation of diverse food sources such as flying insects, crawling arthropods, fish, lizards, birds, rodents, other bats, nectar and pollen, fruit, and blood. Bats pursue these diverse food sources in likewise diverse habitats that range from deserts to dense forests and from open air spaces to highly confined environments. Solving the sensing problems that are posed by these different objectives and constraints requires a system that is adaptive as well as robust.

The basic function of bat biosonar has obvious parallels with technical sensing approaches, especially sonar and radar, but also biomedical diagnosis based on ultrasound. It has long been noted that there are parallels in signal design, in particular between biosonar and radar [2,70,71], where in both cases frequency-modulated waveforms (“chirps”) are applied to increase bandwidth while at the same time allowing for a longer signal duration with sufficient energy.

Beyond these basic similarities, there are notable differences between the approaches taken by bat biosonar on one side and technical sonar or radar on the other. Modern sonar and radar systems are based on the concept of array signal processing [27], where the output signals from a large number of channels are combined.

The characteristics of the entire sonar or radar device are then adjusted through the combination of the individual channels. As a consequence, the individual elements in the array can have very simple device characteristics. On the emission side, arrays are typically used to create a narrow beam through which the radiated power is radiated is concentrated within a small range of directions. On reception side, the goal of array signal processing is likewise to concentrate receiver sensitivity within a beam that is as narrow as possible. The ability of an array to deliver a narrow beam is determined by the overall size of the array relative to the employed wavelength. The larger the array, the narrow a beam it can produce for any given wavelength. In addition, the spacing to the individual emitting or receiving elements in the array has to be adjusted based on the wavelength. Taken together, these two constraints lead to array solutions in sonar and radar that are characterized by a large number of simple elements that are distributed over large area.

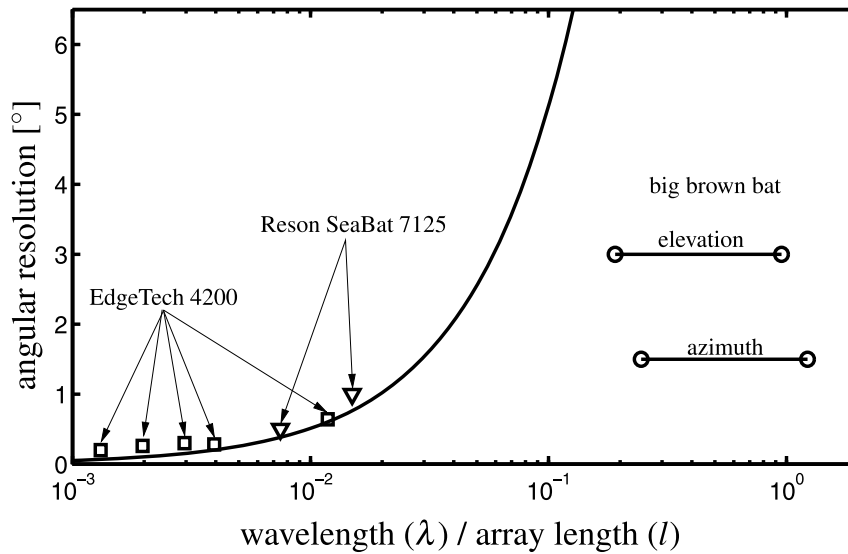
Because bats are small flying mammals, the evolution of their biosonar could not follow the technical paradigm of distributing a large number of elements over a large area. Instead bats have only a minimal number of emitters (one mouth or two nostrils) and receivers (two ears) distributed over a distance that never exceeds a few centimeters. However, the emission and reception elements have much more complexity than the elements in technical radar and sonar. This suggests the hypothesis that bats use element complexity as an alternative strategy to large arrays in order to meet their sensory information needs.

## 2 Sensory information encoding problem

For any sensory system, its interfaces with the external world are of critical importance. This is because any relevant information must be encoded at these interfaces to be available for processing at later stages. Internal system stages dedicated to information extraction or control based on sensory inputs have no direct access to the external world and can hence cannot access information that has not been passed down to them. In engineering, sensing is frequently regarded as a problem that falls primarily into the realms of signal processing and controls. The initial encoding of sensory information into the input signals has either received much less attention or an attempt is made to collect large amounts of raw data indiscriminately, i.e., using a laser scanners, from which the important information is to be extracted at a later stage. Looking at the complexity of the interfaces in the biosonar system of bats gives the impression that the evolution of this system has had a substantial impact on the interfaces and hence leads to the hypothesis that biosonar function relies heavily on the primary encoding of sensory information at the interface stages than its man-made peers.

## 3 Performance gap

Since biosonar allows bats to navigate and pursue prey in complex environments where the success of man-made autonomous systems has yet to be demonstrated, it is probably safe to assume that bats still command a large performance gap over man-made sensing systems designed to solve similar tasks, but this performance gap is hard to quantify in general. However, there is a simple example where quantitative comparison between bat biosonar and technical sonar can be carried out: angular resolution. In an angular resolution task, a sonar system has to distinguish between the magnitude of two different angles that are subtended by targets. The performance in such a task can be determined with trained bats that are asked to select, e.g., the



**Fig. 1.** Angular resolution as an illustration of the performance gap between bat biosonar (Big brown bat, *Eptesicus fuscus*, azimuth resolution [67], elevation [35]) and its man-made peers (EdgeTech 4200 with optional MP technology, in high definition mode [14], Teledyne Reson SeaBat 7125, receive beamwidth [60]). The solid curve is the minimum achievable beamwidth as a function of the ratio of wavelength ( $\lambda$ ) and array length ( $l$ ) given by  $2 \arcsin(0.446 \frac{\lambda}{l})$ .

target with the smaller angle [67]. For one bat species, the big brown bat (*Eptesicus fuscus*), it was found that the animals could distinguish differences in angle down to about 1.5 degrees with 75% accuracy in the horizontal [67]. For the vertical direction, animals from the same species were able to distinguish about 3 degrees [35]. As described above, man-made sonar arrays create a narrow beam to scan their environments. Hence, their resolution for determining the angular positions of targets is given by their beamwidth. The same applies then to determining the angle subtended by two targets. Since the minimum beamwidth that can be produced by an array is determined by the ratio of the wavelength employed and the length of the array, it is also possible to predict the best performance that an array can achieve in the angular resolution task (Fig. 1). Specification data obtained from commercially available sonars [14,60] was found to follow this minimum resolution closely. These systems achieve beamwidths between 0.2 and one degree at wavelength-to-array-length ratios that fall into the range of  $10^{-3}$  to  $10^{-2}$ . In contrast to this, bats have much higher wavelength-to-array-length ratios ( $10^{-1}$  to  $10^0$ , i.e., 10 to 100 times that of the man-made sonar systems in Fig. 1) and much wider beams [4,11,42,54]. For the big brown bat (*Eptesicus fuscus*), for example, -3 dB monaural beamwidths ranging between about 30 and 120 degrees (depending on frequency) have been reported [4]. These values are in agreement with the much larger wavelength-to-array-length ratios in the bats, but they do not match the animal's angular resolution performance. For the same species, angular resolutions of 1.5 degrees in the horizontal (azimuth, [67]) and 3 degrees in the vertical (elevation, [35]) have been reported. These angular resolution values are much below the minimum beamwidth that would be possible given the wavelength-to-array-length ratio of the bats (Fig. 1) as well as their actual beamwidths.

Although the angular resolution of the bats is much better than would be predicted based on their wavelength-to-array-length ratio and hence end up well below the

minimum resolution curve in Fig. 1, it is unlikely that the animals have been able to break any fundamental physical laws. Indeed, the large beamwidths that have been reported for bats [4, 11, 42, 54] show that this is not the case. Instead, this finding should be interpreted as evidence that the bats have found different information sources that allow them to solve the angular resolution task. For angular resolution in the vertical, it has been shown that the outer ear, in particular the tragus [35, 44, 76, 77], generates elevation-dependent spectral cues.

For sensing tasks such as angular resolution tasks where solutions with a well-understood physical basis already exists, the discovery of new information sources from the study of bat biosonar could offer insights into how these problems could be solved under constraints such as on the size of the sensor. Novel bioinspired physical mechanisms that lend themselves to the encoding of sensory information are of even greater interest for sensing in structure-rich natural environments. Such sensing environments continue to pose often insurmountable challenges to technical sensors. Operating active sensing systems such as sonar and radar in environments with many distributed sound-reflecting facets results in so-called “clutter echoes” that cannot readily be interpreted in terms of the geometric arrangements of the contributing targets. Unless tomographic methods [3] based on large numbers of echoes collected from many different directions can be used, reconstructing the geometry of a clutter-target remains an ill-posed problem. However, it has been demonstrated that useful information, in particular with regard to target class can be gained from such echoes by treating them as realizations of random processes and estimating parameters of the underlying probability distributions [46], which can even be done using basic properties of signaling in the nervous system [43]. Classification abilities for stochastic echoes have been demonstrated in bats [22] and a neural correlate has been reported [16]. However, beyond classification of natural targets, it is not clear which sonar sensing capabilities bats have or need to deal with the clutter echoes returned from natural environments.

## 4 Horseshoe bats

Horseshoe bats (family Rhinolophidae) are made up of a single genus (*Rhinolophus*) with about 70 species [13] that are distributed widely in the Old World, including Africa, Eurasia, New Guinea, and Australia. The closely related Old World leaf-nosed bats (family Hipposideridae) have similar number of species and ranges. Horseshoe bats are known for their ability to hunt in dense vegetation [28, 53]. Vision does not seem to play much of a role in providing the sensory information for these capabilities since horseshoe bats have small eye diameters (less than 2 mm, [52]) and their large noseleaves are placed to obstruct parts of their field of view.

To cope with their dense, structure rich environments, the biosonar system of the horseshoe bats must be able to provide information for navigation tasks such as obstacle avoidance and landmark recognition as well as tasks related to hunting such as prey detection and tracking. At present, prey detection is by far the best understood of these tasks and has produced evidence for a wealth of adaptive mechanisms in horseshoe bat biosonar. The fundamental problem of prey detection for horseshoe bats hunting in dense vegetation is to distinguish the echoes from potential prey (e.g., a moth or a beetle) from echoes that were generated by reflecting facets in the vegetation, in particular leaves that are often similar in their sizes and planar geometries to the wings of a prey insect. Horseshoe bats solve this problem in a dynamic fashion: They detect the Doppler shifts that are induced by the wing motion of the prey [29, 64]. Since reflecting facets belonging to the vegetation have much lower speeds than the wings of a flying insect, the Doppler shifts provide a distinguishing

feature that is reliable enough to detect a prey insect even in the presence of clutter from a much larger number of leaves. However, since the wing-beat speeds of insects are small compared to the speed of sound, the biosonar system of the horseshoe bats had to undergo several evolutionary adaptations to detect them. The signal design of horseshoe bats has been adapted for the detection of Doppler shifts through the introduction of narrow-band (“constant-frequency” or cf.) components [41] that provide a precise frequency marker. The vocal tract of horseshoe bats also shows adaptations for producing high-amplitude, narrowband signals [24, 57, 58]. Detecting the small frequency shifts in these narrow-band signal requires a high frequency resolution that is achieved through specializations in the inner ear (cochlea) [30, 33], its innervation [8], as well as in the brain [55, 66]. These specializations lead – or are hypothesized to lead – to a higher frequency resolution, but only in a narrow frequency band that is called an “acoustic fovea” in analogy to the fovea of the retina. Given the narrow bandwidth spanned by this fovea ( $\sim 4.5$  kHz [51]), horseshoe bats need to compensate [63] the Doppler shifts that are introduced by their own motion [72]. Hence, horseshoe bats make use of a dynamic control system [38] to place the returning echoes into a frequency band where they have the necessary resolution to detect the Doppler shifts.

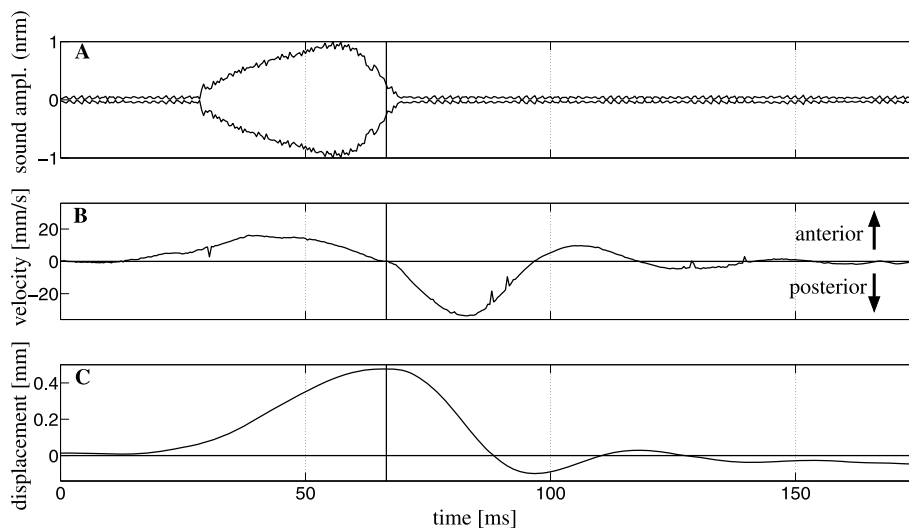
## 5 Emission

Horseshoe bats are able to produce fairly high emission levels, around 100 dB SPL at a distance of 68 cm have been reported in the laboratory [65]. The biosonar pulses are generated using the vocal folds in the larynx following a basic mechanism that is shared with human speech. The pulses then exit through the nostrils, which is not the case for all bat species, but is also found in other major bat families, in particular the closely related Old World leaf-nosed bats and the New World leaf-nosed bats (Phyllostomidae), as well as in some smaller bat groups (false vampire bats, Megadermatidae and slit-faced bats, Nycteridae). At the interface between the nasal tube and the free-field, horseshoe bat biosonar emission employs elaborate baffle shapes, so-called noseleaves. The noseleaf diffracts the outgoing ultrasonic wave packets and through this process determines the distribution of the emitted acoustic energy as a function of direction and frequency. This function is referred to as a “beam pattern”. Beam patterns are usually normalized to a maximum gain of unity and can be used to describe the distribution of receiver sensitivity as well. For greater horseshoe bats, laboratory measurements have determined of an overall -3 dB-beamwidth of about 50 degrees in the horizontal and 90 degrees in elevation [65], which is inline with beamwidths across other bat species [11, 42, 45, 54].

Horseshoe bat noseleaves consists of three parts: anterior leaf, sella, and lancet. The anterior leaf is an incomplete horn with a concave surface profile that surrounds the frontal part of the nostrils. The sella [78] is a straight peg that protrudes in the anterior direction immediately posterior to the nostrils and hence completes a circular baffle that surrounds the nostrils. The lancet is not positioned immediately adjacent to the nostrils, but is separated from the emerging sound fields by the sella. Nevertheless, it often has a complicated structure with half-open cavities that have been shown to influence the distribution of the emitted ultrasonic energy over direction [23, 73, 80, 81] through a resonance effect [80].

### 5.1 Emitter dynamics

Beyond the static geometrical complexity provided by the three components of the noseleaf and their shape features, the emitter interface of the horseshoe bat biosonar



**Fig. 2.** Example of the noseleaf dynamics in horseshoe bats: motion of the anterior leaf in synchrony with the emission of a biosonar pulse. A) Envelope of the ultrasonic pulse (normalized to maximum amplitude), B) surface velocity of the anterior leaf recorded with laser Doppler velocimetry, C) displacement of the anterior leaf surface (obtained through integration of the velocity signal shown in B) [15].

system also has a dynamic dimension. The anterior leaf has been shown to dynamically change its shape in tight temporal synchronization with the emission of the biosonar pulses (Fig. 2), [15]: With the start of pulse emission, the wall surfaces of the anterior leaf start to move inwards (in the anterior direction) thereby increasing the curvature of the horn baffle. The walls continue to move inwards for the entire duration of the pulse; they reset with a quick motion in the opposite direction immediately after the pulse. Since the motion of the anterior leaf is bilaterally symmetric, the aperture of the baffle changes by about one millimeter, which is equivalent to about one quarter of the wavelength of the narrow-band portion of the animals' biosonar pulses. The bats appear to have control over the motions of the anterior leaf walls and can turn the motions on and off. No correlation of the motion amplitude with the emitted sound pressure level was found [15] which suggests that the motions are not a byproduct of pulse emission, e.g., as motion introduced by heavy breathing. While these experiments were made with the greater horseshoe bats (*Rhinolophus ferrumequinum*), the motions of the anterior leaf are conspicuous effects that can be seen in horseshoe bats of all sizes, ranging from one of the smallest species in the family (least horseshoe bat, *Rhinolophus pusillus*) to the largest (woolly horseshoe bat, *Rhinolophus luctus*). In a species belonging to the close related Old World leaf-nosed bats an elaborate muscular actuation apparatus of noseleaf has been described [20] that is likely to be also present in horseshoe bats.

In addition to the dynamics of the anterior leaf, it has been reported that greater horseshoe bats can also move their lancet during the emission of biosonar pulses [25]. In the case of the lancet, the motion takes the form of a rotation about the lancet base [25]. Like the motion of the anterior leaf, lancet motions were found to occur during pulse emission but the timing was not as strictly synchronized as for the anterior leaf [25]. Numerical estimates of the beampatterns associated with different lancet rotations have predicted significant alterations to the animals' emission beampattern as a result of the rotations [25]. Numerical results have also predicted an interplay

between the action of the resonance cavities in the lancet and the overall rotation of the lancet: The furrows were found to create a narrow beam in the upright position of the lancet but enhance the distribution of pulse energy into secondary maxima upon forward rotation of the lancet [23].

In parallel with the dynamic effects that have been observed in the lancet elements, an acoustic dynamics in the emission beam of horseshoe bats has also been reported in the Japanese horseshoe bat (*Rhinolophus ferrumequinum nippon*) [37]: It was found that the beamwidth of the animals increased as they closed in on their prey by more than 20 degrees in the horizontal and more than 10 degrees in the vertical. This has been interpreted as an adaptation to increasing angular displacements that result from relative motion between the bat and the prey with decreasing distance [37]. The physical mechanisms behind these changes in beamwidth have yet to be determined, but it should be noted that these changes in beamwidth occur on a substantially larger time scale than the reported motions of the noseleaf parts: Whereas the beampattern changes occur in a gradual fashion over multiple pulses emitted during the approach [37], the motions in the anterior leaf [15] are always completed within the duration of a single pulse. The rotations of the lancet are a more flexible and can occasionally be drawn out over two subsequent pulses, but are usually also completed before the start of the next pulse [25]. Hence it still remains to be seen what mechanisms are responsible for the gradual adjustments of the beamwidth during the approach phase and what the acoustic correlates of the fast noseleaf changes in a behaving animal could be.

## 6 Reception

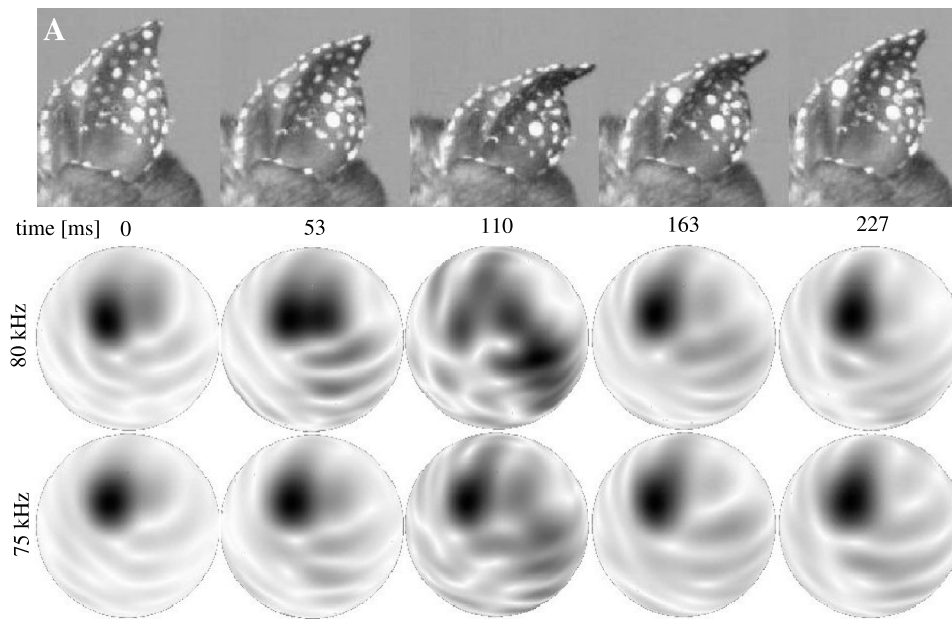
The outer ears (pinnae) of horseshoe bats are large compared to the animals' head sizes. In the greater horseshoe bat (*Rhinolophus ferrumequinum*), for example, the mean skull length is 20 mm and the pinna length 22 to 23 mm [13]. The length of the pinna has been found to be weakly inversely correlated with pulse frequency, i.e., the lower the frequency range used, the larger the pinnae [79]. Besides their relative size and forward orientation, horseshoe bat pinnae are characterized by three prominent local shape features: a large and conspicuous antitragus, a vertical ridge along the anterior rim of the pinna, and a “washboard pattern” of horizontal grooves and ridges on the inner pinna surface posterior to the vertical ridge. The overall receiver beampattern of greater horseshoe bats was determined to have a -3 dB-beamwidth of about 40 degrees [21]. However, since the animals have a large dynamic range between their emission levels of about 100 dB SPL and their hearing thresholds around 0 dB SPL [36], horseshoe bats should be able to receive echoes and distinguish spectral features from a wide range of directions [19].

### 6.1 Receiver dynamics

The pinnae of horseshoe bats are notable for their elaborate muscular actuation apparatus: Whereas the “basic mammalian” pattern consists of just four ear muscles that connect the pinna to the skull, the horseshoe bat pinna is has about 20 muscles, many of which are entirely located on the pinna [62]. Contraction of muscles that terminate on the pinna with both ends must necessarily lead to a deformation of the pinna shape. Hence, this specializations of the pinna musculature suggest that dynamic pinna motions and pinna deformations in particular are important to the biosonar function of horseshoe bats.

Experimental evidence has shown that ear motions have an impact on the ability of horseshoe bats to avoid obstacles along the vertical dimension [40]. After cutting a





**Fig. 3.** Example of the outer ear (pinna) dynamics in horseshoe bats: conformation changes in the pinna (A, frames from a high-speed video recording with artificial point markers placed on the bat ear) and numerical beampattern predictions for frequencies of 75 (B) and 80 kHz (C). The beamgain amplitudes are coded linearly by the gray value from 0 (white) to 1 (black) [18].

facial nerve (*N. retroauricularis*) that innervates muscles on and behind the pinna as well as the tendons of four large ear muscles, the ability of the bats to avoid horizontal wire obstacles decreased from 90% to 75%. The effect of horseshoe bat ear motion has been modeled as a scan of the environment in which the location of the target can be determined from the pinna orientation for which the largest echo amplitude is returned [74]. However, besides their overall rotation components, the pinna motions in horseshoe bats have a strong deformation component. Over a typical pinna motion cycle in greater horseshoe bats, the tip of the pinna is bent down by about 20% of the total pinna height [18]. These non-rigid deformations happen on a very short time scale where the transition between a fully upright pinna conformation and a bent conformation where the pinna tip has been displaced downwards by 20% of the pinna height can happen in as little as 100 ms. Numerical beampattern estimates of (Fig. 3) predict that the changes in the shape of the pinnae in greater horseshoe bats have a profound, quantitative as well as qualitative, changes to the beampattern of the bat. For the upright configuration of the pinna, the estimated beampatterns were dominated by a single sensitivity maximum (“mainlobe”), whereas the beampattern predictions for the bent pinna configuration showed pronounced secondary maxima (“sidelobes”). Furthermore, the mainlobes and the sidelobes that were created through pending of the pinna tip showed a different dependence on frequency. Whereas the mainlobe changed comparatively little with frequency, the pattern of sidelobes that were associated with the bent pinna configurations was strongly dependent on frequency.

Although it is not yet known if these qualitative changes in beampatterns with pinna bending have a function and if so, what this function could be, the different properties of the beampatterns would a good match for different sonar sensing

tasks [18]. Monaural direction finding requires direction-dependent spectral signatures, i.e., the received echo spectrum should be subject to a thorough transformation with direction [47]. In contrast to this, target identification requires that the original echo spectrum and the target information that it contains are passed through by the pinna with as little alteration as possible. The nature of the different beam-pattern types predicted for the bent and the upright conformations of the pinnae fit the requirements of target direction finding and target identification respectively. For the upright pinna conformation, the mainlobe orientations in the beampatterns over the entire frequency band used by the bats were found to be aligned. Hence, echoes from targets located in region covered by these mainlobes would pass a flat transfer function. In contrast to this, echoes impinging within the region covered by the sidelobes in beampatterns of the bent pinnae would be transformed by a transfer function with peaks and notches that would depend on the exact direction of the target. Obviously, the requirements for target localization and identification cannot be both met by the same beampattern. This means that either a decision in favor of one or the other sensing task has to be made or a compromise between the requirements of the tasks has to be struck [59]. Given this situation, it could be hypothesized that the horseshoe bats use the deformation of their pinna to alter between a beampattern that is well suited for direction finding and another that is optimized for target identification.

## 7 Biomimetic reproductions

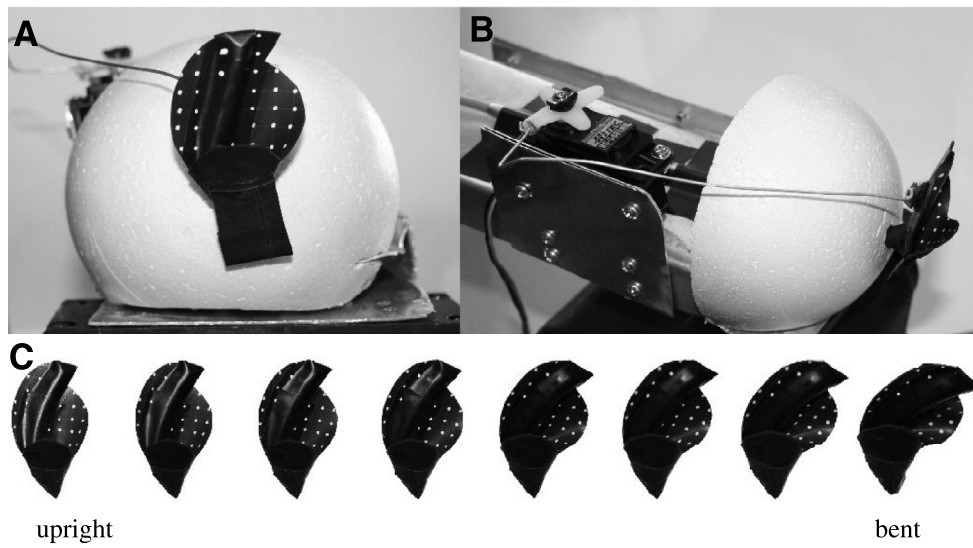
The dynamic function of the horseshoe biosonar system are difficult to investigate *in vivo*. The characteristics of a dynamic sonar system depend on direction represented by two orthogonal angles such as azimuth and elevation, frequency, as well as time. Measuring these four-dimensional functions in a living animal would require a large number of repetitions of exactly the same biosonar dynamics, e.g., in order to test sounds from across a dense enough sample of the direction space. To address this issue, biomimetic reproductions of bat biosonar can be used to explore the impact of different static and dynamic sonar features experimentally.

Whereas early biomimetic sonar systems [6, 31, 32, 49, 74] incorporated only motion of the entire sonar head or rigid rotations of the ultrasonic transducers, systems specifically inspired by horseshoe bat biosonar have attempted to recreate the shape dynamics of the horseshoe bat pinna using actuation of flexible baffles (Fig. 4, [48, 50]).

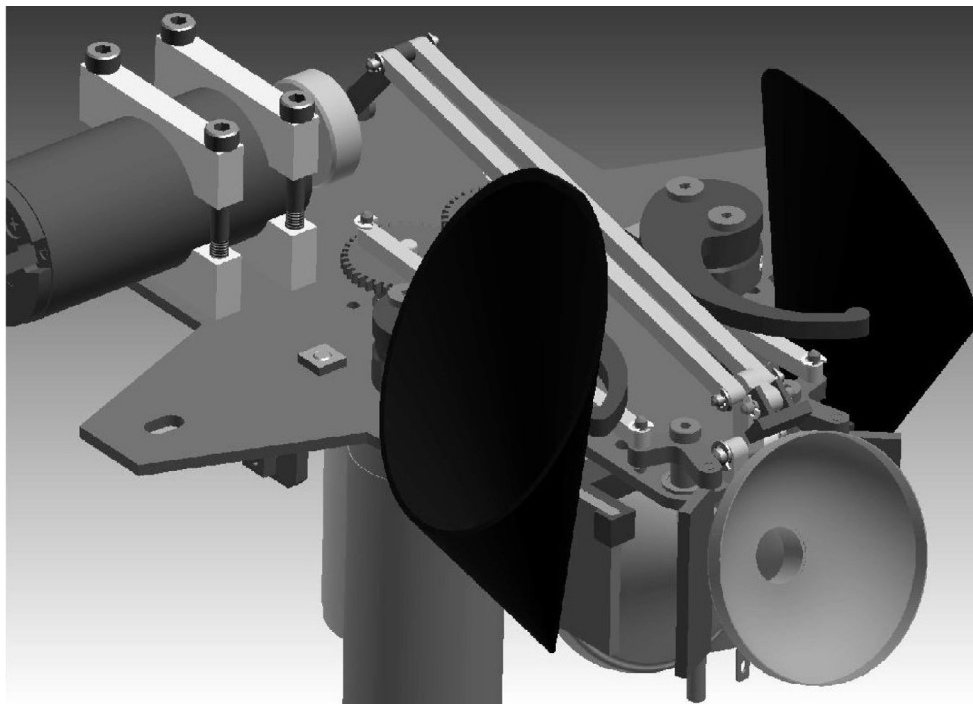
Experimental characterizations of these devices have produced good qualitative agreement with the numerical predictions made for the beampatterns of the dynamically deforming horseshoe bat pinna [18, 56] and have hence demonstrated the feasibility of the biomimetic approach. Furthermore, high-resolution four-dimensional device characterizations obtained for such systems have revealed even stronger dynamic effects in the time domain that would have been visible using standard frequency-domain device characterizations of selected individual conformation stages that cannot capture transients between the analyzed stages or do not preserve them if they fall within the integration time window of the Fourier transform [39].

In addition to confirming the numerical predictions and revealing an even greater degree of time dynamics, these biomimetic devices have also enabled in-depth investigations of the link between form and dynamic function [56]. It was possible to determine that static shape features of the horseshoe bat pinna (antitragus, vertical ridge, and a lateral incision into the pinna rim) interacted with each other and the dynamic change in shape conformation to create a dynamic beampattern [56].

Whereas the first biomimetic sonar head designs with flexible baffles [48, 50] were limited to simple one-point actuation of the pinnae, the next-generation of biomimetic



**Fig. 4.** Biomimetic sonar head with a simple actuation mechanism for the pinna: A) frontal view of the pinna mounted on a hemisphere as a replacement for the head, B) side view showing the simple actuation mechanism used, C) dynamic pinna shape deformation sequence controlled by one-point linear actuation of a flexible pinna shape (isobutyl rubber) [56].



**Fig. 5.** Design for a next-generation biomimetic sonar head with noseleaf and pinna dynamics. The noseleaf and pinna shapes shown in the design are placeholders that do not reproduce any of the geometric features seen in their horseshoe bat equivalents.

devices currently under development seeks to implement reliable, multi-degree of freedom actuation of emission as well as reception baffles ([10], Fig. 5). These devices are aimed at the creation of dynamic ultrasonic signatures upon emission as well as reception.

## 8 Conclusions & outlook

The biosonar of horseshoe bats is an exceptionally capable biological sensing system that holds promise for the discovery of dynamic physical principles that are not currently used in engineering. While the basic physics of, e.g., sound propagation, diffraction, and echo formation is well understood, the impact of adding a dynamic dimension to these processes on information encoding in an active sensory system still remains to be understood. While investigating this topic may not yield new fundamental laws of physics, it could result in new insights how dynamic extensions of known physical laws could be leveraged to transform the way in which sensory systems encode information about the world. A paradigm shift to more powerful dynamic sensing would be very timely since it coincides with an increasing need for smarter, more capable sensing technology that can deal with structure-rich, unpredictable natural environments.

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