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Exploring the dynamics of mammalian vocal-motor processes with emerging advanced technologies

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Abstract

Biomimetics involves looking to nature to find new or alternative solutions to human problems. Man-made sonar is one technological example where a half-century of independent development has led to many advanced implementations. Despite the basic similarities with animal echolocation, biosonar is still far ahead of the performance curve due to its superior imaging in dense clutter, rejection of jamming, adaptation to new environments, and sheer simplicity of having only two receive sensors. We still cannot explain the incredible precision of echolocators nor create manmade devices of comparable performance. Until recently, insufficient recording technology has been the main limitation in the field of biosonar research. Today, advanced sensing and data processing allow for more powerful and economical recording devices, which are accelerating our understanding of animal biosonar. This article summarizes recent technological advances in biosonar and applications of new technologies that provide innovative engineering solutions in this interdisciplinary field.

Keywords: Biosonar, Echolocation, Biomimetics, Bioacoustics, Vocal-Motor Processes

Introduction

Organisms that use sound for sensing their environment face the challenge of a complex and chaotic auditory scene. In order to correctly process and respond to acoustic stimuli organisms must successfully isolate target sounds from background sounds, or acoustic “clutter” [1]. Microchiropteran bats, which use echolocation for navigation and foraging [2], provide excellent models for investigating mammalian auditory processing. During flight, bats produce brief ultrasonic signals and use the corresponding echoes to localize, discriminate, track, and capture prey with fine precision [3, 4].

The spatial directivity of a transmitted sound is described by the beam pattern, which maps the frequency dependent amplitude versus angle in azimuth and elevation. The emission beam of the echolocation signals is spatially broad, which provides an advantage of a large acoustic imaging area. Similarly, the receive beams of each ear are also broad in angle, enabling bats to be aware of their entire immediate surroundings. However, these broad beams come with a trade-off: Echoes from background objects or sonar signals of conspecifics arrive simultaneously from many different directions [5, 6, 7]. Unwanted interference signals can disrupt the perception of targets by masking echoes of interest and have negative implications for foraging [8].

Despite these challenges, bats have adapted and actually thrive in cluttered environments. They can navigate a variety of complex habitats [9, 10, 11, 12], select prey that are located near or on background vegetation [3, 13, 14, 15], and successfully forage in groups of actively echolocating conspecifics [13, 16]. Additionally, bats display remarkable resolution in both, range and angle. Behavioral studies have shown that bats are able to discriminate objects in range within about 1 mm [17, 18] and resolve objects in angle down to 1.5 degrees in azimuth [19] or 3.0 degrees in elevation [20].

A fundamental question in biosonar is how, with broad echolocation beams, can bats discriminate between simultaneous echoes from targets and clutter and demonstrate such fine angular acuity? The answer lies, in part, with the spatio-temporal structure of their emitted beam. Some bats produce frequency-modulated (FM) downsweeps with energy in frequencies between approximately 20 and 100 kHz. Because sound beams generally narrow as frequency increases, this results in an emitted beam with a frequency gradient relative to the main axis of the echolocation beam (Figure 1). If the bat directs the main axis of its beam towards the target, it receives echoes with relatively equal energy from all frequencies (such as with the beetle in Fig. 1), but if it directs its beam slightly off-axis, it can receive echoes with variable energy from different frequencies (such as the moth in Fig. 1), which may provide more information to the auditory system than an echo with constant energy across all frequencies.

Some bats have demonstrated this behavior in laboratory settings. Instead of pointing the main axis of their echolocation beam directly at a tethered insect, Egyptian fruit bats instead alternate directing their beam slightly left and slightly right of a target [21]. By doing so, they direct the echolocation beam off-axis to the side of the insect, which provides better localization of the target.

This frequency-dependent feature of the bat's echolocation beam is also useful for segregating clutter from targets in complex environments. In natural foraging scenarios, bats receive echoes not only from the target of interest but also from clutter in the nearby environment. If clutter objects are located at the same distance as the target, bats will receive echoes from both objects simultaneously. If bats relied solely on temporal cues to detect targets, the clutter echoes might be classified as target echoes, or even mask the perception of targets. Instead, bats use spectral cues from echoes for distinguishing targets from clutter. In laboratory psychophysical experiments, bats were trained to respond to test echoes, simulating on-axis targets, while additional echoes simulating clutter were simultaneously presented with different delays and spectral characteristics [8]. Based on these experiments, it was determined that when clutter is located off the main axis of the echolocation beam the returning echoes contain different frequency components than target echoes, and bats may exploit these changes in beam structure to improve angular resolution and accuracy [8].

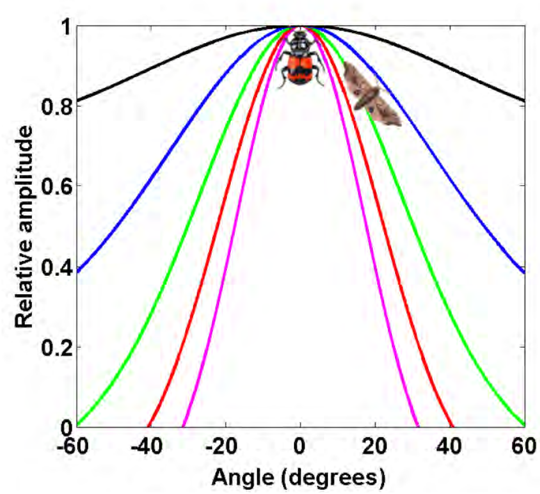

Figure 1: Example of angle-dependent frequency gradient in an emitted echolocation beam. Because the beam narrows as frequency increases, there is an angle-dependent frequency gradient as targets get further off-axis. Targets located directly in front of the bat at zero degrees (represented by the beetle) reflect equal energy across all frequencies. Targets located slightly off-axis (represented by the moth) reflect variable energy depending on frequency.

In addition to exploiting the frequency gradient inherent in their emitted echolocation beams, some bats adjust frequency characteristics of their echolocation signals from pulse to pulse, adapting their vocal-motor output depending on environment or condition. Bats dynamically adjust the width of their echolocation signals, which might further be a strategy of reducing echoes from unwanted clutter [22, 23]. The narrower the beam, the less echoes the bat will receive from objects that are located off the main acoustic axis. Some bats that produce constant-frequency (CF) signals exhibit Doppler shift compensation, adjusting the frequency of their emitted signals depending on flight velocity to maintain a constant received echo frequency [9]. Other bats produce strobe groups, pairs of pulses with alternating short and long pulse intervals [15]. Although the exact function of these strobes groups is unknown, they are most often produced in highly cluttered environments and might be used to obtain information from variable ranges: the short pulse interval may provide information from objects near the bat and the long pulse interval may provide information from the extended acoustic environment [15]. The second pulse of a pair is often emitted prior to receiving the first pulse's echo, which might lead to confusion over which echo corresponds to each emitted pulse. To avoid such pulse-echo ambiguity, some bats slightly adjust the frequency of pulses within a strobe group [11]. Many species of bats appear to have evolved a unique and diverse set of adaptive echolocation techniques.

These modifications of pulse characteristics occur on a timescale of a just few milliseconds, and are important for the bat to successfully perceive its auditory environment. In order to further investigate and understand mammalian auditory processing, new and innovative approaches are needed for gathering information on the adaptive, dynamic, vocal-motor processes in echolocating bats. Today's researchers are at the forefront of the technological revolution in measurement and computing. Advanced sensing and data processing capabilities have become more powerful, miniaturized, and lower in cost than ever before. This article provides an overview of some recent successful demonstrations with these new technologies and offers insight on applying innovative engineering solutions to new areas of biosonar acoustics research.

Recent Technological Advancements

One of the most perplexing issues in bat biosonar is that behavioral and field data are still insufficient to explain the incredible biosonar performance of echolocating bats in clutter. Dynamic behavior, such as echolocation waveform design and beam pattern adjustments, appear to play a large role in bats' ability to acoustically focus on interesting targets while maintaining awareness of obstacles off-axis. This lack of data in the field and laboratory is due mainly to technological limitations. New technologies, approaches, and analyses are shedding light on how the mystery of the bat's incredible echolocation performance can be understood.

Recent studies in the literature have demonstrated an improved set of methods for understanding adaptive echolocation techniques by echolocating bats, whales, and dolphins. A primary reason for this recent burst in dynamic behavioral studies is the improved resolution and sampling of recording devices available. In order to detect and understand the fine-scale, subtle changes in bats' biosonar vocal-motor system, a recording system is needed that is highly accurate, resolvable, and repeatable. Distributed arrays of microphones allow researchers to reconstruct the spatio-temporal structure of bats' echolocation beams. This beam pattern structure is not only defined by azimuth and elevation, but also critically depends on frequency, due to the broadband nature of these signals, and time, since acoustic baffle structures such as the ears and mouth are constantly moving. To visualize this multi-dimensional acoustic information with sufficient fidelity requires a very large number of sensors and supporting equipment to sample the space. Ideally, these detailed acoustic beam measurements should be made with high quality, precision calibrated microphones, which have a flat frequency response, low directivity, and excellent gain and phase matching. All of these characteristics are important for accurately measuring the broadband sound field relevant to animal echolocation, which spans over a decade of frequencies in many cases.

Unfortunately, high-cost ultrasonic microphones have historically limited the resolution of recording arrays. Recent developments in microelectromechanical systems (MEMS) offer a low-cost solution to the beam pattern measurement problem. One of the earliest applications for MEMS sensors was in the automotive industry as low-cost accelerometers for airbag deployment. Since this early success, MEMS technology has matured significantly and is now found in a broad range of other applications, most notably in cellular phone microphones [24]. MEMS is appealing for many sensing applications, because many mechanical structures can be miniaturized and produced on the same integrated silicon substrate as the connected electronic circuitry (Figure 2). Ultrasonic MEMS microphones, which are 2 to 3 orders of magnitude lower in cost that precision ultrasonic microphones, provide a low-cost, omnidirectional, commercially-available solution that can be assembled in dense arrays to provide new insight into the near-field acoustics in close proximity to biosonar structures.

New and creative approaches to designing arrays with advanced technologies have recently enabled high-density acoustic sensing systems with up to 224 ultrasonic microphones and a spatial sampling resolution between 3 and 6 degrees [25]. High density beam measurements have also appeared underwater for marine mammals [26], although low-cost MEMS ultrasonic sensor technology has yet to transition into that realm [27, 28].

Large-scale sensing requires that many concurrent requirements are met: Numerous spatially distributed sensors, sufficient bandwidth and synchronization of data acquisition equipment, adequate transfer speed to data storage, and automated software for rapid online or offline data analysis. Without meeting these requirements, researchers will spend less time searching for evidence of adaptive echolocation techniques and more time finding ways to compensate for the limitations imposed by their experimental design.

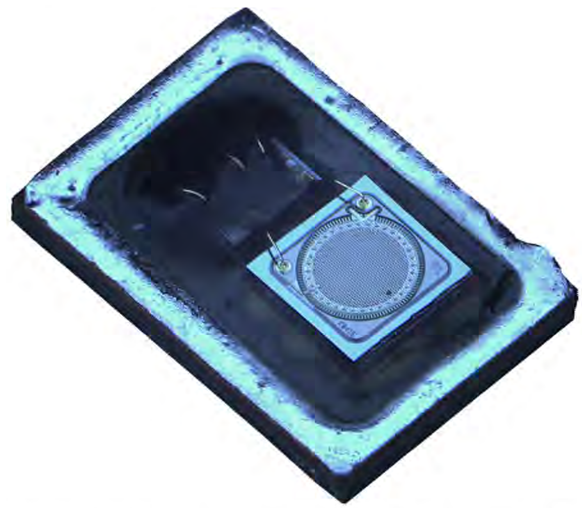

Figure 2: Close-up photograph of a Knowles Acoustics MEMS microphone with the wind screen absent. The pressure sensing surface is the small, approximately 1 mm diameter circle at the center of the MEMS substrate. Acoustic waves actuate the surface of the sensor and small changes in capacitance are translated into electrical signals that can be amplified and conditioned. Bonded wires carry the electrical signals to and from the supporting integrated circuit (covered by the black protective coating) and the entire unit can be automatically assembled by machine onto a custom printed circuit board. Photo is courtesy of Knowles Corporation, with permission.

Until approximately a decade ago, large-scale acoustic measurement systems would be nearly impossible to construct without a substantial research budget. Aside from the large cost of pressure sensors and their associated electronics (i.e. preamplifiers, analog-to-digital converters, transceivers, memory storage), the collection of data across hundreds of sensor elements requires synchronized control of variable-gain amplifiers and analog-to-digital converter devices. Commercial devices exist that can implement these solutions for applications requiring tens of channels recorded simultaneously, but not for the hundreds of channels in emerging biosonar arrays. One solution to this challenge is to employ field programmable gate arrays (FPGA), which allow custom digital hardware to be easily replicated across all channels simultaneously [29, 30]. FPGAs do require a working knowledge of digital circuit design principles; however, all of the hardware is built from a software description rather than a firm set of dedicated circuits.

In addition to new approaches to investigating the sounds of bats, new technology has enabled sophisticated analysis of the anatomical structures involved in sound emission and reception. By creating detailed three-dimensional representations of these structures, morphological and numerical models can be applied to further understand the role of anatomy and help create biomimetic structures. Microcomputed tomography (micro-CT) creates fine-resolution scans of objects, and combined with reconstruction software creates tomographic representations of anatomical structures [31]. From these boundary layer reconstructions, various numerical methods can be applied to investigate the role of specific structures in shaping both the incoming and outgoing sonar beam [32, 33, 34, 35, 36]. Although micro-CT models are useful for numerically investigating the potential role of structures in echolocation, they do have limitations in that preserved specimens are typically used and as such, deformations may not be accurate. Micro-CT can be done *in vivo*, although the current frame rates are probably insufficient for bat echolocation studies. In addition, micro-CT models can be fused with in-vivo recordings to obtain reproductions of natural shape-change behaviors [37].

With a high-resolution micro-CT model, the possibility exists for replicating the physical structure and performing acoustic experiments to either validate the computational modeling estimates, or analyze the sensitivity of the structure to small perturbations in shape. Before high-resolution 3D printing was available, stereolithography, laser sintering, and waterjet cutting were common methods of choice to recapture 3D structures, but the materials may generally be too rigid to adequately model reflectivity of animal tissues. The cost of these and many other modern 3D printing technologies remain high, but some studies have recently appeared that use this method successfully [38, 39]. As the cost of 3D printing and associated CAD tools reduce and the quality of the devices improve, 3D printing will undoubtedly increase in popularity for many aspects of acoustic research.

Studying the adaptive role of acoustic structures in echolocation requires close observation with an advanced set of visual tools. Echolocation acoustic structures appear to change shape on both, the macro-scale of minutes during a behavioral task and micro-scale of milliseconds for an individual pulse [40, 41]. In order to observe changes on such a broad time scale, high-speed and high-resolution video is necessary. Furthermore, to eliminate any visual cues in the echolocation task, all experiments with physical targets must be conducted in the dark. Swapping out the camera lens for one with the Infrared filter removed is the standard working solution. Infrared illumination of the subject then provides an easy method for viewing subjects in the dark. The cost of such equipment has reduced significantly with recent technology advances. Currently, low-cost cameras are commercially available that can record up to 240 fps at full HD resolution (1920 x 1080 pixels) or better. These cameras are also sufficiently compact that arrays of these devices may be used to reconstruct a multiscopic 3D reconstructed view. To supplement these data, laser Doppler vibrometry can be conducted in concert with video and acoustic recordings to measure precise deformations in acoustic structures during specific phases of sound emission from live specimens [42].

Conclusions

Bioacoustics is a highly interdisciplinary field that remains ripe with new discoveries to be made. The advancement of technology has been critical to a commensurate advancement in bioacoustic research and it will continue to be. Embracing new technologies allows both biologists and engineers to work together in achieving new feats of scientific merit.

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