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Using array technology to understand dynamics of echolocation in bats and toothed whales

Laura N. Kloepper, Ph.D.
Brown University Department of Neuroscience, Providence, RI
UMass Dartmouth Department of Electrical and Computer Engineering, Dartmouth, MA
email: laura_kloepper@brown.edu

Abstract
Echolocation, a unique sensory strategy of projecting and receiving ultrasonic signals to perceive the environment, is a dynamic process used by bats and toothed whales that allows the emitter to adapt its sound to environment and echolocation task. This paper reviews the application of acoustic array sensing to understand echolocation dynamics in Microchiroptera and Odontoceti.

Introduction

Echolocation, or biosonar, is a sensory modality that evolved independently in both microchiropteran bats (family Microchiroptera) and toothed whales (suborder Odontoceti). Because bats primarily forage during the night and odontocetes often forage at depth of limited light, these animals developed a unique strategy to the challenges of hunting for prey in an environment with very little ambient light. Instead of relying primarily on vision, these animals emit short, intense, ultrasonic sounds and use the reflected echoes to navigate and locate prey.

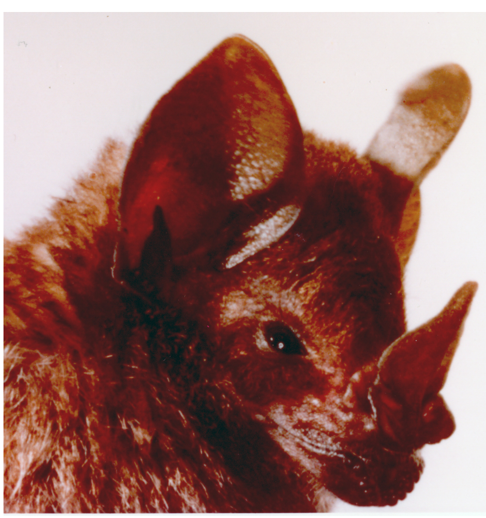

Figure 1: Photo of *Carollia perspicillata*, a nose-leaf bat. Sound is projected from the nose-leaf structure which helps create the shape of the sound beam. Photo credit: Mark Terk.

Microchiropteran bats produce their echolocation sounds in their larynx and emit them through either their nose or highly developed noseleaf structures (Fig. 1). The signals are typically 1 to 25 ms in duration, with frequencies between 20 and 110 kHz [37, 10, 20, 34]. The echolocation calls of bats are species specific and can be frequency modulated (FM), constant frequency (CF), or a combination of both. Odontocetes, on the other hand, produce their signals pneumatically using highly specialized nasal structures [40, 31, 11, 22]. Some groups of species produce FM sweeps or low frequency signals, but the most of the odontocete species produce short, high frequency signals (for purposes of this paper I will further only refer to these groups, the Delphinid and Phocoenid families of Odontoceti). Inside the forehead lie a pair of structures called the monkey lips dorsal bursae (MLDB) complex. Each MLDB contains a valve-like structure composed of dense tissue (the phonic lips) and a pair of fat bodies (the dorsal bursae) [11]. To produce sound, odontocetes pass high pressure air across one or both of the phonic lips which causes the lips to slap together and create echolocation pulses [12, 26, 29, 13]. These pulses are directed through a fat-filled melon, and emitted into the water from the anterior forehead (Fig. 2) [1, 3]. These signals are typically 10 to 70 μs in duration, with frequencies between 25 and 130 kHz [35]. Delphinids produce signals with most energy in a range of approximately 80 kHz (termed broadband), and phocoenids produce signals with most energy in a range of approximately 20 kHz (termed narrowband) [2, 17, 5, 35, 46].

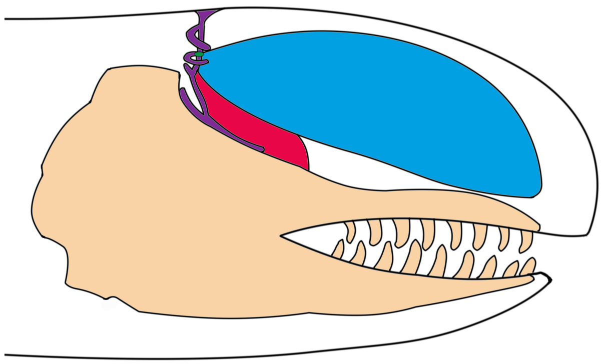

Figure 2: Schematic of the sound generation apparatus for a false killer whale. Green= MLDB complex, red= nasal plug muscle, purple= air sacs, blue= melon, beige= bone.

Directionality of Echolocation Signals

Despite differences in echolocation producing structures and call type, these two groups of mammals both produce signals that are directional, meaning they do not emanate equally from all directions of the animal and have a measurable sound beam. Due to the nature of sound, higher frequency sounds will have a greater directionality (or a narrower sound beam) than lower frequency sounds [19]. This directionality is key to the design of the echolocation system: by producing signals with a narrow range of ensonification, the animal can increase the amount of energy reflected back from a target of interest and decrease the energy reflected back from surrounding clutter.

Regardless of the initial directionality produced by the animal, all sound beams will spread as they are transmitted through a medium such that the sound beam will cover a larger area as the distance between the animal and the target increases. As such, a narrow sound beam will be beneficial for reducing echoes from clutter while tracking prey at long ranges, but might be disadvantageous for tracking prey at narrow ranges, especially if the prey is able to make evasive maneuvers [39, 42, 41]. If the sound beam is sufficiently narrow, any movement by a prey item at close range might put the prey outside the area of the sound beam and render it acoustically invisible to the echolocating animal. Therefore, there is an inherent tradeoff between creating a sound beam narrow enough to reduce clutter at wide ranges yet broad enough to track prey at close ranges. A strategy of dynamically changing the width of the echolocation beam according to the distance of the prey target or degree of clutter would counteract these effects.

Recently, research with both bats and odontocetes suggest that these animals might be able to do just this. These changes in beam angle, size or shape might be accomplished by manipulating structures responsible for sound production and beam shape formation. As mentioned above, depending on the species either the mouth or the noseleaf serves as the acoustic emitter for bats. Experiments demonstrate that changes in the mouth opening or noseleaf shape can dramatically alter the emitted beam shape, so the bat can make rapid, fine scale adjustments in the shape of these structures to manipulate the directionality of the echolocation beam [21, 49, 50, 45, 44]. With odontocetes, it is hypothesized that they use their melon, which is composed of unique acoustic fats, to help focus the emitted sound [14]. The melon contains a topography of fats with variable sound speed transmissions that direct sound towards the front and center of the melon, where it is then transmitted into the water [27, 36, 30]. This melon is surrounded by a vast network of muscles that may act to change the curvature of the melon and change the directionality of the emitted beam much like an acoustic lens [18].

Acoustic Array Sensing Technology

One of the biggest challenges in any scientific field is developing research equipment and methods that are reliable, precise, easy to replicate and affordable. Research with echolocating animals is no exception. Animal vocalizations are measured using microphones (in air) or hydrophones (in water). These devices are electroacoustic transducers that, on the simplest level, convert acoustic energy to electrical energy. Most microphones used for bat research are condenser microphones, which provide an electrical signal as sound waves displace a diaphragm located inside the microphone case. An emergent sensor technology known as micro electro-mechanical systems (MEMS) are quickly becoming popular in the design of bioacoustics arrays [15]. Known best for their use in cellular phones, low-cost MEMS devices are commercially available in a wide variety of frequency ranges and sensitivities. These MEMS devices have the advantage that they can be as effective as many larger microphones but are a fraction of their size. By measuring the tiny capacitance change between two interleaved fingers, MEMS devices can produce a voltage response to the sound pressure waves received by the exposed silicon die.

Most hydrophones are composed of materials with piezoelectric or electrostriction properties, meaning they gain an electric charge when they receive a physical stress (such as a sound wave impinging on the element). To measure the sound at one location, only one receiver, or element, is needed; however, to capture the echolocation beam shape, multiple receivers are needed. This is accomplished with an array of elements in a known geometric configuration. Common array configurations include linear arrays, y-shaped arrays, or planar arrays and may be densely or sparsely populated (Fig. 3).

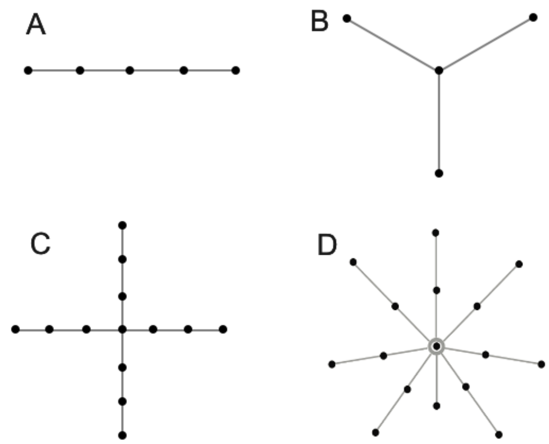

Figure 3: Examples of common array configurations. A) linear array, B) y-shaped array, C) cross section planar array, D) radial planar array.

The process of recording and reconstructing the beam shape is relatively simple. All of the calibrated elements in the array simultaneously record each echolocation signal. Once the signals have been recorded, the beam reconstruction occurs via off-line analysis. For each signal, the element with the highest recorded amplitude (in units of db SPL re 20μPa for air and dB SPL re 1μPa for water) is considered the center, or "on-axis" element, for that signal. The amplitudes are then calculated for the remaining elements of the array and the beam angle, size, or shape is calculated via interpolation between the array elements.
In order to quantify the beam, a criterium must be set for amplitude values. Typically, a -3dB limit is set relative to the on-axis element and defined as the main lobe emitted by the animal. For example, if the on-axis element has an amplitude value of 180 dB, the -3dB beam would be the elements (or interpolated value between the elements) where the amplitude is 177 dB. Because the decibel scale is logarithmic, the -3dB portion of the beam represents the area with half the power of the on-axis signal. For linear arrays, this -3dB value is typically given in azimuth and elevation angles assuming a symmetric beam shape. For planar arrays, these values can be given in terms of beam area, which

allows for asymmetric beam shapes (Fig. 4).

Applying array sensing as a biological research tool

The basic structure and design of acoustic arrays allows for measurement of biological signals under a variety of conditions in the laboratory and the field. For odontocetes, some of the most commonly used field array designs are linear and Y-shaped arrays (Fig. 3A and 3B). These arrays can be stationary or towed off boats to localize individuals and measure the echolocation signals of free-ranging animals [32, 9, 28]. While field arrays provide great insight into the foraging behavior of wild odontocetes, arrays used in laboratory settings allow for fine scale measurements of the beam in a controlled environment. Perhaps the most basic information is that of beam shape. Although some species of odontocetes, such as the false killer whale (*Pseudorca crassidens*) produce a single-lobed, symmetric beam [25], others, such as the bottlenose dolphin (*Tursiops truncatus*) produce a beam with a dual-lobed structure [43]. This is thought to aid in tracking prey and might be achieved by using both sets of phonic lips for sound production. The phonic lips of some odontocetes are asymmetric and it is thought that low-frequency signals are produced by the larger right side, high frequency signals are produced by the smaller left side, and the two signals are combined within the melon [7, 26, 13, 43]. Some bats, such as the big brown bat (*Eptesicus fuscus*) also produce a beam with a dual-lobed structure, and although the mechanism is unknown, it its thought to aid in altitude determination [16]. Instead of pointing the main axis of their beam at their target, Egyptian fruit bats (*Rousettus aegyptiacus*) use a strategy of directing the maximum slope of their beam at the target, which is likely optimizes target localization [48]. Although this has not yet been directly tested in odontocetes, prior measurements of echolocation beam direction show some species direct their echolocation beam slightly upwards or downwards which might indicate a utilization of slope for target detection. For example, the -3dB echolocation beam has been measured at an upward angle of 5 degrees for the beluga whale (*Delphinapterus leucas*) [8], upwards angles of both 5 [6] and 20 degrees for the bottlenose dolphin [4], 0 degrees for the harbor porpoise [5], and a downward angle of 5 degrees for the false killer whale [7]. These differences in beam direction might be a result of species specific differences in skull anatomy [11] or might be due to active beam steering during echolocation [33].

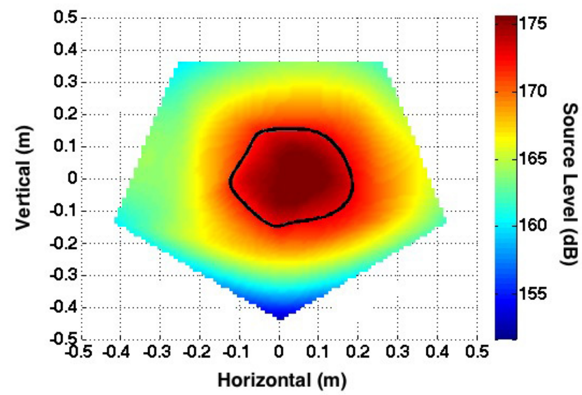

Figure 4: Recreation of the echolocation beam via the interpolation method for a radial planar array. The color bar represents the source level, or intensity of the signal interpolated across the area sampled by the array. The black line indicates the -3dB contour of the beam and the beam area can be calculated from this shape.

In addition to understanding the basic shape of the echolocation beam, array measurements allow for a more intricate investigation into how the beam changes during different echolocation scenarios. For example, Daubentons bats (*Myotis daubentonii*) have been shown to narrow their echolocation beam while searching for insects in the field versus in the laboratory [44]. This increase in directionality occurs with a concomitant increase in signal intensity and might be accomplished by increasing the width of the mouth opening during echolocation. Producing louder, more directional signals has a benefit for bats flying in the field: more energy is concentrated in a narrower direction, which results in stronger echoes from targets of interest and quieter echoes from surrounding clutter. Such a strategy is likely employed by odontocetes as well, as echolocation signals from free-ranging individuals tend to have higher directionality than laboratory individuals [47, 38]. Adjustment of beam width is not limited solely to echolocation environment, and recent studies indicate that both bats and odontocetes can change their beam depending on the target distance or direction. Both Daubentons bats and Serotine bats (*Eptesicus serotinus*) widen their echolocation beams during the terminal phase of echolocation [23]. Widening the beam when prey are close allows bats to compensate for the disadvantage of a directional beam and would increase the probability of prey detection at close range. False killer whales change the size of their beam depending on target characteristics or distance which might be a strategy of reducing the size of the beam to maximize the energy in the reflected echo [24]. Perhaps even more remarkable is evidence that bottlenose dolphins can widen and even steer their echolocation beam depending on angular target location, which further suggests internal beam control via structures associated with the melon [33]. With the array studies to date, we are only beginning to get a glimpse of the capability of the fine acoustic adjustments performed by these animals during echolocation. As computing power increases and cost of equipment decreases, the amount of information available from array technology will become more detailed and allow for further in depth investigation into the dynamics of echolocation.

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