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ECHOLOCATION IN DOLPHINS WITH A DOLPHIN-BAT COMPARISON

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ABSTRACT

Dolphins possess a highly sophisticated auditory system and a keen capability for echolocation. Signals are emitted in the form of high intensity, short duration, broadband exponentially decaying pulses. The frequency spectra of echolocation signals used by many dolphins are dependent on the output intensity of the signals and not on any fine tuning by the animals. When the output intensity is low, the center frequency of the click tends to be low. As the output intensity increases, the center frequency also tends to increase. The pulses propagate from the dolphin's melon in a relatively narrow beam, and echoes are received via the lower jaw, with a slightly wider beam. Echolocating dolphins can detect targets at ranges of approximately 100 plus meters, depending on the size of the targets. Target discrimination experiments have shown that dolphins can discriminate the shape, size, material composition and internal structure of targets from the echoes. The broadband short duration properties of the signal allow the echoes to have high temporal resolution, so that within the structure of the echoes a considerable amount of information on the properties of the target can be conveyed. A brief comparison between the bat and dolphin sonar system will also be made. Bats typically emit much longer signals and a wider variety of different types of signals than dolphins. Signals used by some bats are suited to detecting Doppler shift, whereas the dolphin signal is designed to be tolerant of Doppler effects.

Key words: dolphin echolocation, bat echolocation, echolocation signals, target detection, target discrimination, detection threshold, discrimination threshold

INTRODUCTION

Dolphins emit sounds and analyze returning echoes to detect and recognize objects underwater, a process referred to as echolocation. Acoustic energy propagates in water more efficiently than other forms of energy, so the use of echolocation and passive acoustics (listening) by dolphins is ideal. Dolphins echolocate by emitting acoustic pulses in a directional beam and listening to echoes reflected from objects in their environment. By scanning their echolocation beam across objects and by analyzing the characteristics of the echoes, dolphins can obtain considerable information about their environment. The presence of, size, structure, material composition and shape of objects can be determined. The relative distance of objects can also be determined by estimating the time between the transmission of a pulse and the reception of echoes. Most of the research results discussed here will pertain to the Atlantic bottlenose dolphin *Tursiops truncatus*. Details of this general article are available in my book *The Sonar of Dolphins* by (Au, 1993).

I. ACOUSTIC CHARACTERISTICS OF ECHOLOCATION

a. The reception system

A dolphin's echolocation capabilities are dependent on both their ability to produce high intensity sounds in a controlled manner and on the characteristics of their auditory system, including neurological processing capabilities. Experimental evidence indicates that sound enters through the lower jaw (Bullock et al. 1968, McCormick et al. 1970, Brill et al. 1988). Evoked potential measurements of evoked potentials in the inferior colliculus by Bullock et al. (1968) indicated that the area of maximum sensitivity on the dolphin's lower jaw is forward of the pan-bone area.

In a pioneering study, Johnson (1968) measured the auditory sensitivity of a bottlenose dolphin as a function of frequency. The dolphin's audiogram measured by Johnson is shown in Figure 1 along with the audiograms of a number of different odontocetes. In order to present the audiograms in a single figure with minimum confusion, the original results were curve fitted so that each audiogram would be a smooth rather than a ragged curve. These audiograms indicate that the hearing sensitivity of many odontocetes is very similar, from the large killer whales to the small harbor porpoises. All of the animals could hear high frequency sounds beyond 100 kHz, considerably higher than for most mammals. The bottlenose dolphin can hear over a wide frequency range between 75 Hz to 150 kHz, with maximum sensitivity (within 10 dB) between 10 kHz and 120 kHz.

Johnson (1968) also measured the capability of a *Tursiops truncatus* to detect pure-tone signals in the presence of broadband masking noise. From his masked threshold data, he determined the critical ratio of the bottlenose dolphin as a function of frequency. The notion of critical ratio assumes a pure-tone signal is masked only by a narrow band of noise that is centered about the signal frequency, and the width of this band can be estimated by taking the ratio of the signal power to noise density at threshold. The critical ratio is related to the width of the auditory filter (Flecher 1940). The bandwidth of the dolphin's auditory filter increased almost proportionately with frequency, suggesting that the dolphin's auditory system may be modelled



Figure 1. Audiograms for different cetacean species, *Tursiops truncatus* (Johnson 1967), *Phocoena phocoena* (Andersen 1970), *Orcinus orca* (Bain and Dahlheim 1992), *Inia geoffrensis* (Jacobs and Hall 1971), *Delphinapterus leucas* (White et al. 1978), *Tursiops gilli* (Ljungblad et al. 1982) and *Pseudorca crassidens* (Thomas et al. 1988a).

as a bank of constant-Q filters. A Q ($f_o/\Delta f$) between 12.3 and 14.4 is estimated for the dolphin auditory system (Au 1993). It is this filter property of the dolphin's auditory system which allows the animal to perform frequency analysis of received acoustic signals.

Another important parameter of the dolphin auditory system is the receiving beam pattern, which allows dolphins to localize objects in three dimensional space, to spatially separate objects in a multi-object field, and to minimize the amount of received noise and other interferences. The receiving beam pattern of a *Tursiops truncatus* was measured in the vertical and horizontal planes by Au and Moore (1984). The dolphin's masked hearing threshold was measured as a function of the angular position about the animal's head of either the noise or signal source. The receiving beam for signal frequencies of 30, 60 and 120 kHz are plotted in the vertical plane in Figure 2a and in the horizontal plane in Figure 2b. The shape of the beams in Figure 2 indicates that the beams become narrower, or more directional, as frequency increases. The 3-dB beamwidths in the vertical plane are approximately 30.4° , 22.7° and 17.0° for frequencies of 30, 60 and 120 kHz, respectively, and 59.1° , 32.0° and 13.7° in the horizontal plane.



Figure 2. (a) Receiving beam patterns in the vertical plane for frequencies of 30, 60 and 120 kHz. (b) Receiving beam patterns in the horizontal plane for frequencies of 30, 60 and 120 kHz. The relative masked thresholds as a function of the angle of the signal source are plotted for each signal frequency (from Au and Moore 1984).

There is also an asymmetry between the portion of the beam above and below the dolphin's head. The shape of the beams drops off more rapidly as the angle above the animal's head increases than for angles below the animal's head. If the dolphin receives sounds through the lower jaw, the more rapid reduction in hearing sensitivity for angles above the head may be caused by shadowing of the received sound by the upper portion of the head structure.

The ability to localize or determine the position of a sound source is important for a dolphin in order to resolve the relative position of targets within the echolocation beam. Renaud and Popper (1975) examined the sound localization capabilities of a *Tursiops truncatus* by measuring the minimum audible angle (MAA) in both the horizontal and vertical planes. The MAA measured in the horizontal plane shows a U-shaped pattern, with a value of 3.6° at 6 kHz, decreasing to a minimum of 2.1° at 20 kHz and then slowly increasing in an irregular fashion to 3.8° at 100 kHz. The region where the MAA decreases to a minimum (about 20 kHz) may be close to the frequency at which the dolphin changes from using interaural time difference cues to interaural intensity difference cues. The MAA in the vertical plane varies almost linearly from 2.3° at 20 kHz to 3.5° at 100 kHz. They also measured MAAs of 0.9° in the horizontal plane and 0.7° in the vertical plane using a click signal with a peak frequency of 64 kHz.

b. The transmission system

Echolocation signals seem fall into two general categories. to Broadband, short duration (< 100 μ s) signals typically used by bottlenose and many other dolphins belong to the first category. Examples of the broadband short duration signals emitted by a Pseudorca crassidens are shown in Figure 3. Four basic types of signals are typically emitted. Type I signals have a single low frequency peak, typically below 70 kHz. Type II signals have two peaks, the major peak being at a low frequency (\leq 70 kHz) and the secondary peak at a higher frequency (> 70 kHz). Type III signals also have two peaks, with the major peak at a high frequency (> 70 kHz) and the secondary peak at a low frequency (≤ 70 kHz). Type IV signals have essentially a single high frequency peak. The source level of the different signals increases from the Type I to the Type IV signals, as can be seen in Figure 3. A scatter plot of center or centroid frequency versus peak-to-peak source level for the signals used by the Pseudorca is shown in Figure 4. The data clearly indicate a strong tendency for the center frequency to increase as the source level increases. The correlation coefficient between the linear regression line and the data in Figure 4 is 0.80. Echolocation signals of *Tursiops truncatus*, Lagenorynchus obliquidens, Steno bredanensis, Globicephala melanea (Evans 1973), Pseudorca crassidens (Thomas et al. 1988b) and Delphinapterus leucas (Gurevich and Evans 1976), measured in tanks, tend to be the Type I and II signals. Peak-to-peak source levels in the order of 170-180 dB re 1 μ Pa are typical for signals measured in tanks (Au 1993). Dolphins tend not to emit high intensity signals in tanks, possibly to avoid receiving high reflections from the tank walls. The short distances associated with tanks may also not necessitate the use of high intensity signals. However, in open-waters, high intensity signals have been measured with Tursiops (Au 1993), Delphinapterus (Au et al. 1985) and Pseudorca (Thomas and Turl 1990), with source levels in the order of 210-225 dB and peak frequencies between 110 and 130 kHz.

Echolocation signals belonging to the second category are narrowband, long duration (> 125 μ s) type typically used by the smaller dolphins such as the Commerson's dolphin, Dall's porpoise, harbor porpoise, and Hector's dolphin (Au 1993). Carder et al. (1995) recently reported that the pygmy sperm whale (*Kogia*) also emits narrow band, long duration echolocation signals. Examples of signals



Figure 3. Examples of echolocation signals emitted by *Tursiops* in the open waters of Kaneohe Bay, Oahu, Hawaii, and in a tank.

in the second category are shown in Figure 5. The frequency content of these signals does not seem to be related to source level. Similar kinds of signals have been measured for these animals in tanks and in open waters (Au 1993). However, these animals do not seem to emit high level signals; the maximum peak-to-peak amplitude measured for any of the five species represented by Figure 5 has been approximately



Figure 4. Scatter plot of center frequency versus peak-to-peak source level (from Au et al. 1995).

165–170 dB re 1 μ Pa emitted by Dall's porpoise in the open ocean (Hatakeyama an Soeda 1990). Peak-to-peak source levels of about 155–160 dB have been measured for *Phocoena* in a tank (Hatakayama and Soeda 1990, Goodson et al. 1995).

Dolphins usually echolocate in a pulse-sonar mode in which the intervals between clicks in a train are usually greater than the twoway travel time for an acoustic signal to travel to the target and back by about 20 to 45 ms (Au 1993). If dolphins process an echo before emitting the next click, then the click interval data suggest a processing time between 20 and 45 ms. There is evidence that the beluga whale, for target ranges greater than 80 m, may use packets of clicks in which the time intervals between clicks in a packet is less than the two-way travel time but the time intervals between packets are greater than the two-way travel time (Turl and Penner 1989).

Echolocation signals are projected from a dolphin's head in a directional beam. The transmission beam patterns in the vertical and horizontal planes for *Tursiops* are shown in Figure 6 along with examples of a single signal measured simultaneously by hydrophones positioned about the animal's head. The beam in the vertical plane indicates that echolocation signals are projected at an elevation angle of 5° above the animal's head in a narrow pattern and are aimed directly forward of the animal in the horizontal plane. The 3-dB



Figure 5. Examples of narrowband long duration echolocation signals of (A) harbor porpoise (from Kamminga and Wiersma 1981), (B) finless porpoise (from Kamminga 1988), (C) Dall's porpoise (from Hatakeyama and Soeda 1990), (D) Commerson's dolphin (from Kamminga and Wiersma 1981) and (E) Hector's dolphin (from Dawson 1988).



Figure 6. Transmission beam pattern of a *Tursiops* in the vertical and horizontal planes. Examples of echolocation signals measured by hydrophones located at different angles about the animal's head are also included. The frequencies denoted alongside each waveform are frequencies where local maxima occur and are listed in order of descending values (from Au 1993).

beamwidths are 10.2° in the vertical plane and 9.7° in the horizontal plane.

The signal waveforms in Figure 6 become progressively distorted relative to the signal on the major axis of each beam. In the frequency domain, the peak frequencies decrease as the hydrophone angle increases away from the major axis. The presence of multipath propagation within the head of the animals is evident in the signal measured at $+15^{\circ}$ and $+25^{\circ}$ for the beam in the vertical plane. The necessity of achieving good alignment between a hydrophone and a dolphin makes it difficult to measure undistorted echolocation signals of free swimming dolphins.

c. Bat echolocation signals

Echolocation signals used by bats are brief sounds varying in duration from 0.3 to 300 ms and in frequency from 12 to 200 kHz (Neuweiler 1990). The structure of bat echolocation sounds is varied and diverse, being both species and situation specific (Pye 1980). In most species the sounds consist of either frequency-modulated (FM) components alone or a combination of a constant frequency (CF) component coupled with FM components. Echolocation signals typically consist of the following elements or of combinations of them emitted as single or multiple harmonics: (1) downward FM sweep with linear or exponential time course (Fm_{down}); (2) CF tone or shallowly modulated tonal element; (3) upward FM sweep with linear or curved time course (Fm_{up}) , which only occurs in combination with other sound elements (Neuweiler 1990). Fm-only signals are brief in duration, varying from 0.5 to 10 ms. The sweep is usually downwards. CF signals are either short in duration, varying from 1 to 10 ms, or quite long, varying from 10 to 100 and sometimes to 300 ms.

Orientation signals in the time domain with their representative spectrograms are shown in the top and middle panels of Figure 7 for three species of bats. The signal of the mustached bat *Pteronotus parnelli* is a long-CF/FM with a strong fundamental at about 60 kHz and a second harmonic. The signal of the *Pteronotus suapurensis* is a short CF/FM with multiple harmonics. *Noctilio leporiunus* (fishing bat) emits two type of sounds, a short-CF/FM and a FM with a second harmonic. The orientation sounds emitted by three other bat species, each representing a different family, are shown in the bottom panel of Figure 7. The signal of the big brown bat *Eptesicus fuscus* and the spear-nose bat *Phyllostomus hastatus* are downward FM sweeps with high harmonics present. The signal of the greater horseshoe bat *Rhinolophus ferrumequinum* is a long CF/FM tone. These indicate that bandwidth of the FM signals can be very wide, extending over an octave. The FM signals used by bats and the click signals used by



Figure 7. Orientation echolocation signals of five species of bat (from Simmons et al. 1975).

dolphins for echolocation are Doppler tolerant (Altes and Titlebaum 1970), so they are not affected significantly by either their own motion or that of the prey. On the other hand, long-CF signals used by some bats like *Rhinolophus* are affected by the velocity of both bat and prey so that echoes can carry Doppler information.

Dolphin echolocation signals do not seem to vary a great deal between species as bat signals do. The broadband short duration signals used by many dolphins seem very similar in waveshape and spectrum if differences in amplitude are taken into account. Broadband short duration signals having peak-to-peak amplitudes greater than about 210 dB look very similar when emitted by the different species. The narrowband longer duration signals used by the smaller dolphins seem very similar in waveshape and spectrum. The use of echolocation signals by bats can best be understood by examining the prey pursuit sequence presented by Simmons (1987) and reproduced in Figure 8. It shows 34 signal emissions for a period of about 1.5 s before the moment of capture. The first three emissions were FM sweeps over a narrow frequency range from about 28 to 22 kHz for the fundamental, and from 56 to 44 kHz for the second harmonic. These signals were used to search for targets when flying in an open area (search phase), and were emitted at a rate of about 5 to 10 pulses per second. When the bat detected the prey, it reacted by emitting a distinctively new pattern of sounds. Beginning with



Figure 8. Continuous spectrogram of a sequence of echolocation signal emission by *Eptesicus fuscus* during a pursuit manoeuver (from Simmons 1987).

emission #4, the FM sweep changed abruptly from shallow to steep, indicating that the insect was detected and pursuit had begun (approach phase). The signal bandwidth widened considerably, with the fundamental component sweeping from 50 to 60 kHz down to about 25 kHz, and the second harmonic sweeping from 100 kHz down to 50 kHz. During the approach phase (emission #4 to #10), both the signals and the intervals between emissions became progressively shorter to prevent the echo and the next emitted signal from overlapping in time. The broadband FM sweeps were probably used by the bat to investigate the features of the target. The pursuit culminated with the emission of signals with very brief FM sweeps and progressively shorter intervals between successive sonar emissions (emission #11 to 34) until the insect was captured.

The signal duration, bandwidth and repetition rate changed considerably between the approach and terminal phases of the bat's pursuit sequence. This type of signal adjustment is not generally seen in dolphin echolocation. Repetition rate increases and signal amplitude decreases, and with a decrease in amplitude, the center frequency will typically decrease as the dolphin closes in on a target. Dziedzic and Alcuri (1977) found that the echolocation signal of *Tursiops* performing discrimination task when swimming towards the targets were а relatively invariant when the dolphin was more than 4 m from the target. But, when the animal-target distance was less than 4 m, they found a spectral spreading of the signal. However, it was difficult to ascertain the orientation of the dolphin with respect to the hydrophones, making it difficult to judge whether the changes were caused by hydrophone orientation changes or deliberate manipulation of the signal spectra.

CF signals used by rhinolophid bats, hipposiderid bats and the mormoopid bat can encode velocity information (Schnitzler 1984). CF/ FM bats can sense Doppler shifts in echoes and compensate for the shifts in frequency of the CF portion of echoes by lowering the emission frequency. This phenomenon is termed Doppler shift compensation. For a bat flying towards a stationary target or towards a prey flying away from it there will be a positive Doppler shift so that the frequency of echo will be higher than the emission frequency and the bat will lower its emission frequency in order to compensate for the Doppler shift (Schnitzler 1984). Doppler-sensing CF/FM bats have highly specialized auditory systems that aid them in sensing the frequency fluctuations in echoes. There is usually a narrow frequency notch of increased sensitivity in their audiogram centered close to the reference frequency. These specialized audiograms are also useful in detecting amplitude fluctuations in echoes caused by fluttering insects. Dolphins do not have any comparable velocity sensing capabilities.

II. ECHOLOCATION CAPABILITIES

a. Target detection

The maximum detection range of two *Tursiops* was determined in Kaneohe Bay by Murchison (1980) using a 2.54-cm diameter solid steel sphere and by Au and Snyder (1980) using a 7.62-cm diameter water-filled sphere. The results of both experiments are displayed in Figure 9 with correct detection and false alarm rates plotted as a function of the target range. The detection threshold ranges (range at 50% correct detection) for the 2.54-cm and 7.62-cm diameter spheres were 73 and 113 m, respectively. The animal's results for the two different targets are relatively consistent if the target strength difference is considered in the sonar equation.

The target detection capability of *Tursiops* was measured by two other techniques. A target was positioned at a fixed range, and the dolphin's capability of detecting it was measured as a function of the level of a wide band masking noise (Au and Penner 1981, Au et al. 1988 and Turl et al. 1986). In another experiment an electronic echo generator was used to simulate a phantom target at 20 m and the level



TARGET RANGE (M)

Figure 9. Dolphin target detection performance as a function of range. The 2.54 cm sphere results are from Murchison (1980) and the 7.62-cm sphere results are from Au & Snyder (1980).

of the echo was progressively made smaller as the echolocating dolphin performed a detection task in a fixed noise field (Au et al. 1988). The results of the three different methods of measuring a dolphin's target detection capability were very similar, after echo energy-to-noise ratio (E_e/N) for the range detection data was determined using the transient form of the sonar equation (Au 1993).

The dolphin's detection threshold occurred at an E_e/N of 7.5 dB (see Figure 10.6 of Au, 1993). The signals in Figure 10 can be used to visualize an E_e/N of 7.5 dB. The top waveform is the echo from a 7.62-cm sphere produced with a simulated dolphin echolocation signal. The second and third waveforms depict the same echo for a 7.5 dB signal-to-noise ratio condition for two different filter bandwidth settings. The largest highlight of the echo is observable in the noisy echo; however, the smaller highlights are masked by the noise and the acoustic quality of the echo was altered. The dolphins could probably hear the largest highlight, but the echo probably did not "sound" like the sphere echo they were trained to detect, and consequently reported the target as not present.



Figure 10. Target echo in noise at the dolphin's detection threshold.

Maximum detection range: Bat

Kick and Simmons (1984) measured the target detection capabilities of two *Eptesicus fuscus* using nylon spheres with diameters of 0.48 cm and 1.91 cm as targets. The performance of one bat with the 1.91-cm sphere is shown in Figure 11. The 75% correct response threshold range was 5.1 m. The experiment was conducted in a low-noise environment; the noise level was not measurable. Therefore, the bats' hearing was probably not masked by external noise but by their own internal noise, and it was their absolute threshold for detecting their own sounds that was measured.

The difference in target strength for the 2.54-cm sphere used for the dolphin was only about 2.5 dB greater than the target strength of the 1.91-cm sphere used with the bat. However, the detection threshold range of 73 m for the dolphin is considerably greater than the 5.1 m for the bat, even though the dolphin was limited by ambient noise and the bat was not. One of the reasons for the bat's shorter detection range is related to the high absorption of acoustic energy at ultrasonic frequencies in air. The acoustic absorption coefficient (dB/m) in air is about 100 times greater than in water (Au 1993). Another reason for



Figure 11. Target detection performance of one bat (*Eptesicus fuscus*) in a target detection experiment with a 1.91-cm sphere. Each data point represents 50 trials (adapted from Kick 1982).

the dolphin's longer detection range may be attributed to the dolphin emitting higher energy signals than the bat.

b. Target discrimination

Echolocating dolphins have demonstrated the ability to perform a number of different types of target discriminations. Experiments have been conducted to show that dolphins can discriminate the size, shape, material composition and interior structures of targets. Only three discrimination experiments will be discussed here; interested readers should refer to Nachtigall (1980) and Au (1993) to read about other discrimination experiments.

Material composition and thickness: Dolphin

The first experiment consists of discrimination of the thickness and material composition of metallic plates by Evans and Powell (1967). Dolphins were trained to recognize a 30-cm diam. circular copper disc of 0.22-cm thickness among comparison targets of the same size. The standard copper disc and a comparison target were presented side by side, separated by a center-to-center distance of 50 cm. The dolphin was required to station at the far end of a 9-m tank facing away from the targets. Upon command from the experimenter, the blindfolded dolphin turned and swam toward the target, echolocating along the way. The geometry and typical swim pattern of the dolphins are shown in Figure 12 along with the thickness and composition of the plates and a dolphin's discrimination performance. The three dolphins were able to discriminate the standard from all comparison targets at a performance level of 75% or better except for the 0.32-cm copper and 0.32-cm brass targets.

Weisser et al. (1967) examined the targets by insonifying them at normal incidence using simulated dolphin echolocation signals. There were no indications from the echoes as to how the dolphins performed the discrimination. Au and Martin (1988) also examined the same metal plates using simulated dolphin echolocation signals. They obtained echoes at both normal incidence and at 14° from normal. Backscatter results at normal incidence for the standard copper and three other plates are shown in Figure 13. As with the measurement of Weisser et al. (1967), very little difference could be found in the echoes that allowed the dolphin to discriminate between the plates. However, echoes from the plate at the 14° incident angle were very different from each other, although their amplitudes were about 30 dB less than at normal incidence. The echoes measured at the 14° incident angle contained a reflection from the surface of the plate, and multiple internal reflections caused by the signal penetrating into the plate and





Figure 12. Typical swim pattern of a *Tursiops* during the final 2 m of the plate discrimination and recognition experiment of Evans and Powell (1967). The dolphin's position is given in 1-sec intervals.



Figure 13. Echoes from four of the plates used by Evans and Powell (1967) at normal incidence and at 14° incidence. The echoes at the 14° incident angle were approximately 30 dB lower in amplitude than the echoes at the normal incidence (from Au and Martin 1988).

propagating in a ping-pong fashion between the front and back surface of the plate and reflecting off the edge of the plate (see Figure 9.8 of Au 1993).

Target range difference discrimination: Dolphin

The second experiment to be discussed was conducted by Murchison (1980) and involved the determination of target range difference by an echolocating dolphin. The dolphin was trained to wear rubber eyecups and station in a chin cup that could swivel from side to side, and echolocate two identical 7.62-cm polyurethane foam spheres separated in azimuth by 40° , as depicted in the insert of Figure 14. The dolphin's task was to determine which of the spheres was closer by touching the paddle on the same side of the center line as the closer target. The animal's performance as a function of the difference in the relative target range when the closer target was 1, 3 and 7 m from the front of the chin cup is shown in Figure 14. The 75% correct response



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Figure 14. (a) Target range difference discrimination results, (b) insert describing the experimental geometry (from Murchison 1980).

thresholds were at ΔR of 0.9, 1.5 and 3 cm for absolute target ranges of 1, 3 and 7m. These threshold results correspond to $\Delta R/R$ of 0.009, 0.005 and 0.004 for R = 1, 3, and 7 m, respectively, indicating a very fine range or time resolution capability.

Target range difference discrimination: Bat

Target range difference discrimination experiments with echolocating bats have been conducted by a number of investigators. In the experiment of Simmons (1973) four different species of bats of different genera were used (*Eptesicus*, *Phyllostomus*, *Pteronotus* and *Rhinolophus*). The bats were required to lie on a starting platform and determine which one of two triangular planar targets was closer to the platform. The targets were separated by an azimuth of 40°. The results of Simmons' experiment along with the experiment of Ayrapet'yants and Konstantinov (1974) for *Rhinolophus*, Roverud and Grinnel (1985) for Noctilio and Surlykke and Miller (1985) for Pipistrellus are plotted in Figure 15 in terms of time so that a comparison could be made between the bats and the dolphin *Tursiops truncatus*. The curves indicate that *Tursiops* has a keener time resolution capability than the bats studied so far.

Cylinder wall thickness difference: Dolphin

The third discrimination experiment to be discussed was conducted by Au and Pawloski (1990) and involved a determination of a dolphin's capability of discriminating wall thickness differences of metallic cylinders by echolocation. On any given trial the dolphin was required to echolocate a standard target and a comparison target separated by an azimuth of 22° and located 8 m from the dolphin's hoop station. The dolphin was required to touch a paddle located on the same side of the center line as the standard target. The standard target was constructed out of aluminum with a 3.81-cm O.D., a 6.35-mm wall thickness and a length of 12.7 cm. Comparison targets with wall thicknesses both thinner and thicker than the standard but of the same O.D. and length were used. The dolphin's performance as a function of the difference in wall thickness between the standard and comparison targets are shown in Figure 16. The 75% correct response threshold



Figure 15. Graphs of DT as a function of the two-way travel time T for bats and the dolphin whose results are shown in Figure 14 (from Au 1993).



Figure 16. Dolphin wall thickness discrimination performance as a function of wall thickness difference (from Au and Pawloski 1990).

corresponded to a wall thickness difference of 0.23 mm for the thinner targets and 0.27 mm for the thicker targets. Au and Pawloski (1990) examined the targets acoustically and found that the components of the echo from the front surface and the inside back surface of the cylinders were prominent and the time interval between the first and second reflections was sufficiently different for the standard and comparison targets for the dolphin to perform the discrimination. The difference between the intervals of the standard and comparison targets at threshold was between 0.5 and $0.6 \ \mu s$. Differences in the time intervals between the first and second echo components for the standard and comparison targets also caused the spectrum of the echo from one target to be shifted in frequency in comparison to the other. The amount of shift in spectrum between the standard and the -0.3 mm and -0.2 mm comparison target were 3.2 and 2.2 kHz, respectively.

Hole depth difference experiment: Bats

Two experiments that are somewhat related to the wall thickness discrimination experiment of Au and Pawloski (1990) are the hole depth discrimination experiment with echolocating bats by Simmons et al. (1974) and by Habersetzer and Vogler (1983). The bats were trained to discriminate between the depth of holes drilled into a plexiglass plate. Simmons et al. (1974) trained Eptesicus fuscus to discriminate between holes drilled to a depth of 8 mm and a smaller depth. ranging from 6.5 and 7.6 mm. Their bats could discriminate hole depth differences as small as 0.6-0.9 mm. Habersetzer and Vogler (1983) used Myotis myotis and two reference hole depths, 8 mm and 4 mm. They found that the bat's discrimination threshold was about 1 mm for the 8-mm reference depth and about 0.8 mm for the 4-mm reference The data from these two experiments were in depth. general agreement.

The hole depth experiments with bats produced similar types of cues as the wall thickness experiment with dolphins. The wall thickness difference threshold between 0.23 mm and 0.27 mm is better than the 0.6 to 1 mm for bats. However, since the velocity of sound in water and aluminum for the dolphin experiment is considerably higher than the velocity of sound in air for the bat experiment, the dolphin had to deal with time differences in the order of 0.5 to 0.6 μ s compared to approximately 3.4 to 5.8 μ s. Therefore, it seems that dolphins have a finer temporal resolution capability than bats.

IV CONCLUSIONS

The echolocation capabilities of dolphins have evolved to be extremely well adapted for survival in an aquatic environment. The broadband and short duration nature of echolocation signals allows the dolphin to have very fine time resolution capabilities, even for the smaller dolphins that emit narrower band signals than *Tursiops*. Narrow transmit and receive beams along with spatial localization capabilities allow dolphins to have a good sense of their environment by echolocation or by passive listening. Bats also have good echolocation capabilities that are well suited for the detection, recognition and capture of insects. Their echolocation systems are very different from dolphins because of differences in the environment and type of prey.

There are very little data that can be used to directly compare the differences in the echolocation capabilities of dolphins and bats. Both species have excellent echolocation capabilities suited for very different environments and prey types. The speed of sound in water is approximately five times faster than in air, and this difference should have a large impact on how echolocation is used by both species. Only two types of echolocation signals seem to be used by different dolphin species, whereas the difference in echolocation signals used by different species of bat can be very great. Bats also have a very plastic system in which the signal characteristics can change considerably during different phases of a prey pursuit sequence. This does not seem to be the case with dolphins; although, very little is known about how dolphins use echolocation when foraging for prey. The Doppler shift compensation behavior of some bats is completely missing in dolphins. It may be possible that bats need to extract more of certain types of information such as prey velocity and direction from echoes, because the slow speed of sound in air allows the prey to move some distance between the bat's sound emissions.

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