

Functional Aspects of Echolocation in Dolphins

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“Our perception of how dolphins utilize their sonar in the wild is based on extrapolation of knowledge obtained in ‘laboratory’ experiments—we do not have the foggiest idea of how dolphins utilize their sonar in a natural environment” (Au 1993, p. 271).

Introduction

This chapter surveys some key aspects of the existing knowledge on the functions of echolocation signals emitted by dolphins and other odontocetes, comparing these advances in understanding of cetacean biosonar to those obtained by similar research on bat echolocation. An attempt is made to present the issues requiring clarification, and the topics where fresh empirical research is needed.

Echolocation Signal Characteristics

The echolocation abilities and the signal characteristics of a few odontocete species have been studied in detail. Au (1993, 1997) provided recent reviews especially concerning the bottlenose dolphin (*Tursiops truncatus*), the beluga (*Delphinapterus leucas*), the false killer whale (*Pseudorca crassidens*), and the harbor porpoise (*Phocoena phocoena*). Not all odontocetes have been specifically demonstrated to echolocate, although echolocation-type signals have been recorded from most species.

Richardson et al. (1995) listed 13 species with “echolocation demonstrated” and 17 species with “echolocation-type” clicks. The sperm whale (*Physeter macrocephalus*) was not included in this list, and only indirect evidence exists for the largest of the odontocetes to be considered an echolocator (Mullins, Whitehead, and Weilgart 1988; Watkins and Daher, chapter 57, this volume).

For some species such as the Clymene dolphin, *Stenella clymene*, little is known about their signal production (Perrin and Mead 1994), but it is more than probable that their acoustic characteristics will be similar to those of related species. In other groups, like the ziphiids, information is very scarce. Lynn and Reiss (1992) described click trains recorded in a pool with two young Hubb’s beaked whales (*Mesoplodon carlhubbsi*), but

the equipment was limited in frequency response. Thus the signals may not be representative of the species, and their function was not clear.

Au (1997) divided odontocete species according to their echolocation signal characteristics. Two main categories of signals were summarized: broadband and short (<100 μ s), often with the energy peak, or one of the energy peaks, below 70 kHz; and narrowband, long (>125 μ s), with the energy peak at about 110 kHz. Interestingly, Ketten (1997) found good basis for this gross classification in the anatomy of the cochlea, especially in terms of the basal ratios (thickness-to-width ratio of the cochlear basilar membrane), and even on an ecological basis. In her typology, the first category of echolocation signals presented above is produced by animals with basal ratios between 0.5 and 0.7, functional hearing limits below 160 kHz, and highly social lives with low-frequency communication signals. The second category is more typical of inshore phocoenid and riverine platanistid species, adapted to the needs of fine-detail discrimination in turbid waters. Au (1997) also included smaller delphinids, such as Commerson’s or Hector’s dolphins (*Cephalorhynchus commersonii* and *C. hectori*, respectively), in this group.

The higher intensity signals of the bottlenose dolphin, the false killer whale, the narwhal (*Monodon monoceros*), and the Atlantic spotted dolphin (*Stenella frontalis*) were measured in open water, reaching source levels of 210–230 dB re 1 μ Pa (Au, Herzing, and Aubauer 1998). In contrast, porpoise ultrasonic pulses usually fall below 170 dB (Au 1997), and sperm whale clicks were measured at 180 dB, at frequencies below 16 kHz (Watkins 1980).

In some species, but not all, echolocation clicks were found to be highly directional, with the strongest beam in front of the head, showing a 5° upward tilt. The 3 dB beamwidth (the cone-shaped area with a 3 dB loss compared to the center of the beam) in the bottlenose dolphin was about 10–12° and even narrower (6.5°) in the beluga (Au, Moore, and Pawloski 1986; Au, Penner, and Turl 1987). As these authors noted, the level increment due to directionality can reach 30 dB. This promotes sonar performance for the animal, but makes it harder to obtain the complete spectrum and the highest levels in recordings made at sea, with free-ranging animals.

The high-frequency echolocation components suffer a greater attenuation outside of the strongest beam than the less directional low-frequency components. In species that produce broadband signals, this low-frequency portion of clicks may be detected even when the animal's head is directed at a greater angle from the target. In the power spectra of four bottlenose dolphin clicks, representative of the variability found by Au (1997), one may notice that at 20 kHz (the useful range of many recording systems) the relative amplitudes were at about 70%, 50%, 50%, and 20% compared to the peak.

Distances at which a delphinid uses echolocation signals to discriminate small objects are in the 100 m range in experimental settings (Richardson et al. 1995). However, the disturbing number of accidental entrapments of these animals in fishing nets (Kraus et al. 1997) should alert us to the fact that the abilities demonstrated by trained and focused animals in experimental conditions do not necessarily reflect the spontaneous use of this sensory system in natural, routine situations.

In all species studied, clicks are emitted in trains that vary in duration, number of pulses, and repetition rate (or inversely, interclick intervals). Bottlenose dolphins in stationary discrimination tasks emit each click after the echo of the preceding one is received and processed. Thus, if the distance to the target is incremented by the experimenter, the interclick intervals increase, allowing for the longer two-way transit (TWT) time. There is also a lag time corresponding to the neural processing time. Au (1993) suggested that this processing time should range between 19 and 45 ms.

In observations of dolphins echolocating on objects greater than 1 m away, dolphins tend to adjust the interclick interval so that the echo is returned before the next signal is sent. This ensures that the analysis of the previous click occurs before another outgoing click is sent, perhaps avoiding any masking effect on the weaker echo. In experiments with stationary and moving animals, the interclick intervals of dolphins increased with the distance to the target, allowing for a TWT time (see Au 1980, p. 115, for summary). However, variations do occur, indicating that click rate may have other features currently not understood.

In some species, and within target ranges of less than about 0.4 m, interclick intervals are far too short for this echo-by-echo processing. Trains of 500 clicks per second (interclick interval of 2 ms), so common in some circumstances, could be instances of echo-bulk processing, or could be reserved for other functions, not strictly sensory. One beluga studied by Turl and Penner (1989) performed discrimination tasks using click trains that in some cases did not respect TWT times. Interestingly, the beluga strongly preferred interclick intervals of about 45 ms. It was unclear whether this was an individual peculiarity or a species adaptation. Very high-repetition-rate trains (2 kHz) also were recorded in social situations

with free-ranging Atlantic spotted dolphins (Herzing 1996; Herzing, chapter 56, this volume), orcas, *Orcinus orca* (Ford 1991), Hector's dolphins (Dawson 1991), and, in Sigurdson's (1998) study of moving, echolocating bottlenose dolphins.

This suggests not only that odontocetes use "shorter than two-way transit time" intervals, but that packets of clicks (burst-pulsed sounds) can also be manipulated in an "echolocation way" to provide information to the dolphins. It is unclear whether for odontocetes in their natural environment outgoing signals really mask returning echoes, thus making the very short interclick interval trains less useful for echolocation. Another interesting feature of echolocation, whose function is unknown, were double clicks recorded from pilot whales, *Globicephala* sp. (Purves 1967); harbor porpoises, *Phocoena phocoena* (Verboom and Kastelein 1997); and spinner dolphins (Lammers et al., chapter 58, this volume). Because of the paucity of information from moving dolphins in social contexts, we could have overlooked other processing possibilities of echolocation clicks.

Issues of Signal Design and Discrimination

Echolocation signals of odontocetes operate in a medium where sound travels approximately 4.4 times faster than in air. This property of seawater makes it more difficult to use time-separation cues from echoes and impossible to benefit from Doppler-shift information. Being in air gives bats advantages in this respect. On the other hand, the impedance mismatch between the medium and the targets is lower in water than in air. This enables dolphins to obtain a great deal of information about the inside of targets, while for bats most of a signal's energy is reflected by the surface of the target (Au 1993, 1997).

The research on the discrimination abilities of the bottlenose dolphin's sonar is now in its fourth decade. These studies have revealed unexpected powers of echolocation and a fine adaptation to the properties of their medium. Major reviews were presented by Nachtigall (1980) and by Au (1993), detailing the discrimination of target shapes, such as cylinder length, diameter, sphere diameter, target range, material composition, solid versus hollow targets, and wall thickness and texture. Most studies were conducted with the targets in the water, but a few also tested discrimination abilities for targets buried in sediment (Roitblat et al. 1995 for the bottlenose dolphin; Kastelein et al. 1997 for the harbor porpoise). If targets were buried only a few centimeters, both species were still quite good at discrimination. In the wild, the detection and retrieval of buried prey has been observed (Herzing 1996; Rossbach and Herzing 1997). In addition, the description of foraging techniques specific to prey species and habitat (Herzing, chapter 56, this volume) could indicate that dolphins have the ability to discriminate specific prey species.

The information-bearing parameters in the echoes could be target strength, time-separation cues, spectral (frequency) differences or echo highlight structure. When the acoustic energy of a signal penetrates a target, it creates a series of echo highlights on the inner structures and surfaces. These secondary reflections follow the first echo, produced by the front surface. The very short dolphin clicks allow for detectable differences in the arrival times of the highlight echoes (Au 1993). The number of discernible highlights and the total echo duration are also relevant parameters that echolocating animals could use to discriminate targets. As to target strength differences, one should keep in mind that dolphins can resolve as little as 1 dB differences in echo pressure (Evans 1973).

Research on energetic costs of echolocation production for odontocetes is clearly needed, to advance knowledge at the physiological level and also to allow a better understanding of the ecological, social, and evolutionary aspects of this orientation behavior in these aquatic mammals. Speakman and Racey (1991) measured and monitored the coordinated movements of wing beats and echolocation production in bats, showing the rather economical coupling of the two activities. Bats exhale during the wing upstroke and emit pulses only during exhalation, thereby minimizing the energetic costs of echolocation. Longer pulses are emitted only once per upstroke; shorter pulses are produced in bursts limited to the upstroke. In either case, bats effectively use the energy of the wing beat for sound production.

Echolocation in the Wild: Natural Habitats and Prey

In contrast to the wealth of data on the physical and design characteristics of the odontocete sonar system, little is known about how dolphins manipulate and use echolocation signals in the wild. Food preferences and hunting strategies have been obtained primarily from sampling stomach content (Barros and Wells 1998) and from observations of surface behavior including fish kicking, stranding on mud flats to retrieve fish, and others (reviewed by Shane 1990). Würsig (1986) reviewed general delphinid foraging strategies and surface behavior in different environments. The use of echolocation signals in the detection and retrieval of prey is well established, and intense sound pressure levels of over 220 dB re 1 μ Pa (Au, Floyd, and Haun 1978; Au 1993) emitted by bottlenose dolphins could stun prey (Norris and Møhl 1981), although it has not been experimentally demonstrated. Atlantic spotted and bottlenose dolphins echolocate while scanning and digging for buried prey in sandy bottoms, increasing the repetition rate from 200 to 500 Hz as they direct their sound into the sand (Herzing 1996).

Little is known about the use of echolocation in the dolphin's natural habitats. Critical areas of inquiry for

the future include (1) how a moving dolphin's strategy might vary from a stationary dolphin emitting echolocation clicks, and (2) the possible advantages of using passive audition concomitant with an active sonar system.

How should researchers begin to think about dolphin echolocation in the wild relative to what is known about bats? What parallel features can be compared? Two major ecological features that determine features of bat (Microchiroptera) echolocation are (1) physical environment (cluttered or uncluttered with vegetation or substrate), and (2) prey species—their movement, habitats, and evasive strategies. Although bats show flexibility, their foraging strategies are associated with particular forms of echolocation (Altringham 1996; Fenton 1984). Let's look at these strategies and extrapolate some possible aquatic parallels and comparative aspects with bat ecology.

ECOLOGICAL, ACOUSTICAL, AND BEHAVIORAL PARALLELS

Despite difference in sound velocity and optimum frequency use in aerial and aquatic media, echolocating animals may have encountered similar physical constraints and obstacles regarding environmental clutter and prey movement during evolution. Considering convergent evolutionary strategies and potential parallel adaptations, three main questions emerge: (1) Do dolphins deal with cluttered acoustic environments in the same way as bats? (2) Are dolphins using prey and environmental cues analogous to those used by bats? and (3) Are there parallel passive and active strategies used by both bats and dolphins for prey detection and capture?

Bat strategies: Detection and hunting

Reviews of principles of aerial sound transmission (Altringham 1996; Rydell 1993) suggests that (1) signals that are short, have a wide bandwidth, and are emitted in pulsed series are favorable for the measurement of target distance, angle (localization), and properties (shape, texture); and (2) signals that are long, with a narrow and constant frequency, are favorable for prey detection and trajectory and velocity estimation (Bradbury and Vehrencamp 1998).

Several major features impose tradeoffs in the signal design for various kinds of bat foraging strategies. Open-site foragers need high performance in all aspects: the detection, range and angle estimation, and target properties. Therefore, they send intense signals through the mouth, wide-beam varying with the capture phase: constant frequency–frequency modulated (CF-FM) passing to FM wider bandwidth, faster repetition rate. (As discussed above, with shorter ranges, repetition rate may increase without echoes overlapping with the next signal.)

For hawking (the detection, pursuit, and eating of prey on the move) and fishing bats, on the other hand, the premium is in prey detection and velocity measure-

ment, so they use high-duty-cycle emissions combining FM portions before and after a long CF component. Bats hawking above or between vegetation (uncluttered background) use narrowband FM or CF search calls with no harmonics (15–30 kHz). This ensures early detection over long distances. Upon targeting, hawking bats switch to short, broadband FM pulses to give details of their acquired targets. Bats hawking between vegetation use slightly higher frequency calls since their prey is at relatively shorter distance. Due to echoes from the vegetation clutter, hawking bats use two strategies to reveal their prey against background clutter, both of which involve high-frequency calls (>50 kHz). Some bats use CF calls to detect clutter, others use broadband FM calls with several harmonics as movement detectors.

Gleaner bats (those that glean insects from surfaces like fruit and flowers) also have to fight clutter, and the premium for them is in determining target angle and properties. Therefore, they use short, higher bandwidth, low-intensity calls (hence the epitome “whispering bats”), with narrow beam signals emitted through the nostrils (with nose leaves) for directionality. Gleaning bats over ground/foilage clutter hover over prey and use short (<2 ms) FM echolocation pulses, of low intensity. Their echoes allow the discrimination of texture and targeted movement, over short distances. Many gleaning bats rely on prey-generated sounds and visual contact as alternative senses. Although bats clearly use both active and passive strategies, the details of passive listening in bats during prey acquisition and the use of other cues has not been studied.

Bat strategies: Sound use and prey evasion

Some bats add harmonics in cluttered environments to provide more detail about their surroundings. In uncluttered background situations, fundamental frequencies are emphasized (Simmons et al. 1978). In addition, the use of harmonic structures change during different capture phases (i.e., the approach versus terminal phase). Bats use FM signals in cluttered background environments or during the final approach to a target. FM pulses are good at determining fine structure of the environment. Amplitude modulation (AM) helps determine differences in size. Spectral changes in FM pulses may be used by bats to detect movement in cluttered environments (Altringham 1996). The slightest movement by a prey will change the echo spectrum. This is possibly why bats hover motionless when gleaning, because the movement of the bat itself introduces spectral changes that could complicate analysis.

Bats produce different pulse repetition rates (PRR) during different stages of the capture process (approach versus terminal phases), including a “wind-up” or increase in PRR upon target approach. Increasingly higher repetition rates are associated with insect-catching maneuvers when there is a need to appraise the changing

position of prey. However, when gleaning insects from a surface, bats do not increase their PRRs (Fenton and Bell 1979).

Prey evasion strategies can alter signal use by the predator as well. Insects adjust their “evasion” strategies to intensity and PRR levels by either moving, freezing, or sometimes “jamming” the signals. Moths respond to intense calls by diving to the ground, but they react to less-intense sounds with negative phonotaxes (Roeder 1967). Although bats use different foraging strategies for different prey, they should not be categorized restrictively by the type of strategy alone. In addition, individual differences could be more flexible than previously believed (Fitzpatrick 1980). Bats also share characteristics of information transfer with dolphins, including social signals, imitative learning, eavesdropping, and intentional signaling (Wilkinson 1995).

Dolphin strategies: Detection and hunting

A review of underwater sound principles (such as high sound speed, low absorption) may explain why: (1) Dolphins use very short pulses, high bandwidth, low-duty-cycle pulses, high intensity (actually the porpoises might be called “whispering odontocetes” at 170 dB re 1 μ Pa). (2) Dolphins cannot use Doppler shifts. (3) Binaural localization based on different time delays must be much more difficult but are likely used for low frequencies, and intensity differences for high frequencies >20 kHz (Renaud and Popper 1975). (4) Dolphin prey have body impedances similar to water, so when acoustic energy penetrates, echolocation highlights help discriminate their internal composition. (5) There is no spectral adaptation to specific prey, proximity, or velocity, but dolphins increase click pressure by distance to targets or relative to noise in the environment. (6) Adaptations are made in pulse repetition rate with changing distance to target.

Dolphins inhabit a variety of environments, including rivers, coastal habitats, and open oceans. For animals using echolocation signals in the water with such short wavelengths, anything larger than a few millimeters will be reflected. Therefore, clutter may come in the form of vegetation, rocks, debris, or even bubble screens. Clutter is known to seriously affect echolocation performance in odontocetes, more so at a grazing angle of 90° (perpendicular) than at 68° (Turl, Skaar, and Au 1991). However, these effects have only been studied in artificial situations, and, again, not much is understood about how this factor influences the use of echolocation in the wild. A variety of sensory strategies, including passive hearing, vision, and intraspecific and interspecific behavioral cues, are likely used by dolphins (Wood and Evans 1980). Surface observations of foraging include reports of individual versus group foraging, changing group sizes in open-water versus coastal environments, and varying interanimal distances such as dispersed or

tight school formations (Würsig 1986). The difficulties in obtaining complete spectra, real source levels, and simultaneous underwater observations in free-ranging situations have precluded many studies. Only recently, underwater observations, in at least one clear-water study site, were described (Herzing 1996; Herzing, chapter 56, this volume), and real-time, high-frequency echolocation measured (Au, Herzing, and Aubauer 1998).

Dolphin strategies: Sound use and prey evasion

Echolocation signals of different species of odontocetes vary in structure, intensity, frequency, and pulse repetition rates. Although it is known that dolphins use high-frequency signals, observations on modulated frequency or amplitude, during foraging strategies, are unmeasured. One basic feature, the “wind-up,” or increase in PRR during approach to a target by dolphins (Au 1993), parallels the strategy used by bats.

The coevolution of prey hearing and predator signaling seems to have influenced the design of echolocation signals (Rydell, chapter 43, this volume). Bats form an interesting analogy, since they, like dolphins, can be both predator and prey. Bats and insects have both independently evolved and coevolved. Coevolving strategies include jamming activity, countermeasures, and approach versus terminal stages of hunting both from the predator-detection and prey-evasion aspects. Predators may decrease the probability of alerting their prey by (1) increasing frequencies to extend outside their prey’s hearing range, (2) using cryptic strategies of encoding information within background noise, (3) listening passively and tracking prey, or (4) reducing the intensity or duty cycle of signals.

The ability of prey to detect and adopt evasion responses can influence the “encrypting” of the signal as a strategy as well. Evasion strategies of prey also can be relevant to odontocetes and pinnipeds (S. H. Andersen and Amundin 1976; Thomas, Ferm, and Kuechle 1987). An interesting example is the recent work by Barrett-Lennard, Ford, and Heise (1996) on echolocation strategies by fish versus mammal-eating orcas. This study documented that orcas use passive listening as a primary means of locating prey. They also use echolocation patterns for different hunting strategies—for example, they emit orientation clicks in cryptic patterns (isolated or in occasional doublets), thus masking them in the background noise when hunting other cetaceans (prey that can hear their high-frequency clicks). In contrast, when hunting fish, they do not mask their high-frequency signals.

However, clupeid fish have recently been reported to respond to ultrasound and to simulated dolphin echolocation (Mann et al. 1998), which may be very relevant to dolphins feeding on such species. All extant clupeids share this auditory specialization, preceding the evolution of marine mammal hearing and sound production.

This type of preadaptation is an alternative to the more active coevolution (the adjustment to sensory features and survival strategies) between predator and prey.

It is known that changes in insect “wing” aspect modify the intensity of the echo and lead to amplitude modulation of bat echolocation signals. Bats determine target distance, speed, and size with their echolocation, but echoes also contain insect-specific information of the wing-beat frequency, length, types, and structure, providing prey-species information (Schnitzler et al. 1983). In this case, information is encoded within time intervals and changes in intensity. Could the change of angle of a fish underneath the sand, or moving in the water column, contribute to both prey identification and prey retrieval? Could these cues be used by hunting dolphins? Dolphins could use echolocation to distinguish different prey or learn prey behavior and evasion strategies. Search and approach strategies described by Herzing (chapter 56, this volume) suggest that dolphins not only recognize the type of prey under the sand but also learn the prey’s typical escape mode and employ appropriate strategies to retrieve their meal. Fine-discrimination abilities of dolphins, such as those described by Roitblat et al. (1995), might allow them to select prey by species and size, thus increasing optimal foraging.

Both prey and predator strategies likely will vary with the clarity of water or whether hunting occurs during the day (when vision can also be employed) or at night. Just as bat echolocation coevolved with flight and fast-moving hunting strategies (Rydell, chapter 43, this volume), dolphin echolocation could have evolved due to fast-moving prey. In opposition to their slower moving cousins, large whales, the inner ear structure of odontocetes shows structural changes necessary for high-frequency reception (Ketten 1994). Like bats, dolphins may depend on other senses, including vision and prey-generated sounds, as supplementary cues. In the coastal waters of Florida, fish that are conspicuous sound producers constitute a disproportionate percentage of bottlenose dolphins’ stomach contents (Barros and Wells 1998). Cross-modal work between vision and echolocation in dolphins (Pack and Herman 1995) and bats (Simmons, Moss, and Ferragamo 1990) has illuminated the possibility of shared information between these senses. Insectivore bats may specialize on “groups” of insects (Black 1979) and learn and modify their capture strategies accordingly (Dunning 1968).

ANATOMICAL PARALLELS

Parallel anatomy is another feature we can compare between bats and odontocetes. Both bats and dolphins have low-light nocturnal vision (Bell 1985; Nachtigall 1986) and acoustic lens structures for focusing sound. Bats in the family Rhinolophidae have large, mobile ears to focus reception of signals by rotation, and complex nose leaves that act as an acoustic lens, focusing the

nasally emitted echolocation pulses (Altringham 1996). This nose leaf could be analogous to the dolphin's fatty structure in the head, the melon (Ketten 1994; Cranford, Amundin, and Norris 1996).

Bats and dolphins rotate parts of their body for better sound reception. Bats have the ear/tragus complex that improves directionality to incoming signals and helps focus reception to a field of 30–40° from either side of the midline. Ketten (1994) described the segmented sound-conduction properties of the dolphin rostrum, with the anterior channel specialized for high-frequency reception and the lateral channel for lower frequency reception. This suggests that the mouth and lower jaw are analogous to a hydrophone array, where specific frequency receptors are arranged systematically. If the lower jaw functions as a frequency-specific receptor organ, then we must look at both open-mouth and scanning behavior as potentially proactive searching behavior (Herzing, chapter 56, this volume). Such jaw rotation could be comparable to ear rotation of bats, in its ability to tune and focus reception of frequency-specific acoustic information.

Strategies Using Echolocation

DEFINITIONS OF ECHOLOCATION

Although traditionally categorized separately for their function (echolocation for orientation, burst-pulsed sounds for social interactions), there is no clear demarcation between the production of echolocation and burst-pulsed sounds. Instead, these sounds form a graded series that can be treated as a single class of sounds (Herzing 1988). Perceptual features of click rates, recently reported for orcas (Szymanski et al. 1998), have not been measured for many species.

In addition to the “gray areas” described above, the definition of echolocation by clicks only is challenged by the bat's use of FM sweeps for echolocation (Altringham 1996). In addition, CF-call overlap appears to be an integral part of echo processing in some bats. Although differences between air versus water for the transmission of sound need to be considered, speculations on the function of long-distance, low-frequency, frequency-modulated signals from large balaenopterid whales for an “echo-ranging” function challenge traditional thoughts of the possible uses of FM vocalizations (Frazer and Mercado 2000; Clark and Ellison (chapter 73, this volume). Although echolocation is traditionally thought of as high-frequency sound production, high-frequency sound is not essential for echolocation, as demonstrated in cave dwelling swiftlets who use sound in the 2–10 kHz range (Fullard, Barclay, and Thomas 1993) for gross echolocation tasks. Bradbury and Vehrencamp (1998) reported that oilbirds (*Steatornis caripensis*) emit bursts of clicks with dominant frequencies between 6 and 10 kHz and durations of 1–1.5 s, noting

they probably only detect fairly large obstacles. Similarly, least shrews use audible clicks for echolocation (Thomas and Jalili, chapter 72, this volume). Echolocation aspects of California sea lions, *Zalophus californianus* (Poulter and Jennings 1969), penguins, *Spheniscus humboldti*, and harbor seals, *Phoca vitulina* (Renouf, Galway, and Gaborko 1980) have been reported. However, the predominant view is that these capabilities have not been unequivocally demonstrated by those studies (Richardson et al. 1995). Awbrey, Thomas, and Evans (chapter 70, this volume) provide some new data related to pinnipeds.

Echolocation abilities have been studied in humans, and both the blind and the sighted show unsuspected detection performance using sounds with low dominant frequencies, such as tongue clicks or hisses (Rice, Felstein, and Schusterman 1965). Recently, Arias and Ramos (1997) showed in various performance tests that the ability to detect and discriminate obstacles does not require “privileged ears” or musical training. They used artificial stimuli composed of clicks lasting a few ms, with dominant frequencies below 2 kHz, or noise bursts, also with dominant frequencies below 2 kHz. At distances greater than 3 m, the subjects could hear the emitted signal clearly separated from the echo. At shorter ranges, both sounds fused into a single stimulus but with a perceived pitch shift. This perceived time separation pitch (or repetition pitch) of 200–500 Hz is quite functional for humans, and performance was even better with noise stimuli than with click sounds. Blind humans show greater acuity than the sighted, probably related to their permanent reliance on acoustical cues.

The parallel rules of aerodynamic and hydrodynamic evolution (e.g., moving target detection as reviewed by Altringham 1996) supports the notion that moving target detection may be more complicated than stationary detection (the traditional means of measuring echolocation clicks in dolphins). In one of the few studies of moving echolocation clicks in dolphins, Sigurdson (1998) reported that bottlenose dolphins (1) had variable interclick intervals not necessarily conforming to the TWT time rule, (2) modulated both frequency and amplitude for enhancing signal-to-noise ratios, (3) independently modulated low-frequency and high-frequency components, and (4) optimized their detection abilities through a learning process over time. Echolocation measurements of moving dolphins therefore provide new and important information about the use of this sense in the wild.

PASSIVE LISTENING VERSUS ACTIVE ECHOLOCATION

Dolphins may use a combination of passive listening and active echolocation in hunting. Like bats, dolphins are both predator and prey in their natural environment. Bats, as prey, usually emerge at night in large groups and switch sites to avoid alerting their predators (Altring-

ham 1996). Echolocation may be a secondary or an additional proactive searching technique, after other primary signal detection systems are employed. Fenton (1984) reported that in some cases bats use echolocation to avoid obstacles, relying on other cues for prey detection. Similarly, Barrett-Lennard, Ford, and Heise (1996) suggested that some orcas use click trains only to locate distant obstacles or prey, avoiding emission during the capture approach. When do dolphins and porpoises listen and when do they actively search? These questions are relevant in discussions of mortality reduction in nets (Kraus et al. 1997), and in recent results of the significance of “silence” in wild bottlenose (dos Santos and Almada, chapter 55, this volume) and Atlantic spotted dolphins (Herzing, chapter 56, this volume). The costs of vigilance (usually by active scanning) have been calculated for other species (Illius and Fitzgibbon 1994), but passive listening has not been addressed. Eavesdropping, by individuals or by a group, potentially would facilitate passive listening abilities of wild dolphins, as has been experimentally demonstrated (Xitco and Roitblat 1996). In bats, the need to avoid intragroup mutual jamming may have led to strategies that help to separate calls, but precluded eavesdropping (Obrist 1995).

SOCIAL USES OF ECHOLOCAION

In addition to enhancing foraging abilities and predator detection, echolocation could have a social function, and several authors have found support for this idea (Wood and Evans 1980; dos Santos and Almada, chapter 55, this volume; Herzing, chapter 56, this volume). There remains the additional possibility that the receiver of the buzz is experiencing the tactile effects of sound. Given the graded nature of echolocation clicks and burst-pulsed sounds, it should become apparent that all these sounds may produce a tactile as well as auditory effect.

The genital and mammary regions are the area of richest somatic innervation, followed by the upper rostrum, lower jaw, forehead, flukes, and pectoral and dorsal fins (Ridgway and Carder 1990). Cutaneous mechanoreceptors and their cortical responses were reported by Bullock et al. (1968). Combined with the fact that the trigeminal nerve has the greatest number of axons of any dolphin cranial nerve (Jansen and Jansen 1969), this suggests that acoustic and tactile information are intimately related in dolphins.

What sound-intensity level would be required to surpass tactile thresholds on the dolphin's body? Kolchin and Bel'kovich (1973) presented threshold levels of tactile sensitivity for the common dolphin, *Delphinus delphis*. These measurements were described and recalculated for sound pressure estimates (Herzing, chapter 56, this volume). It is clear that SPL of echolocation signals for several species (false killer whale at 225 dB, Thomas and Turl 1990; beluga at 222 dB, Au et al. 1985; bottlenose dolphin at 228 dB, Au et al. 1974; Atlantic spotted

dolphin at 210 dB, Au, Herzing, and Aubauer 1998; spinner dolphin at 222 and -220 dB, Schotten et al., chapter 54, this volume) are well above the estimated SPL needed for tactile reception by dolphins.

So dolphins not only may receive social information about the receiver during high-intensity and repetition rate use of echolocation signals, they also may cause tactile sensations via sound pressure. Researchers have speculated that use of such intense sound in close proximity could provide both auditory and tactile “comfort or discomfort.” Concomitantly, burst-pulsed packets of clicks were observed in both conspecific aggression (Overstrom 1983), intraspecific and interspecific aggression (Herzing 1996), and during herding behavior of conspecifics (Connor and Smolker 1996) and fish (Norris and Møhl 1981).

LEVELS OF ENVIRONMENTAL INFORMATION

In their recent review, Bradbury and Vehrencamp (1998) showed that echolocating animals often extract high levels of environmental information from their sonar signals, close to what would be physically and theoretically possible. These authors argued that the obvious lack of comparable sophistication in the information content of social signals cannot be explained by design or system limitations. Instead, this asymmetry could only be understood with a “game economical” reasoning—that is, considering that in traditional communication there are conflicts of interest between senders and receivers. Only if senders have substantial benefit from providing conspecifics with high levels of environmental information would there be a functional and evolutionary justified selection pressure for the development of richer signaling. The cases where such systems exist, or might exist, and where genetic economics appear to favor such development, remain hot topics for future research.

In fact, if bats avoid eavesdropping on echoes by conspecifics (Obrist 1995), the picture in the case of dolphins is not so clear. The multitude of communication modes used by these animals may provide conspecifics with details of important features of the environment, and eavesdropping on conspecific echolocation may be the norm rather than the exception. This could explain the null correlation between group size and number of click trains emitted found in bottlenose dolphins (dos Santos and Almada, chapter 55, this volume). Johnson and Norris (1994), having observed the echolocation behavior of spinner dolphins, also suggested that these animals rotate sonar duties in their groups, allowing each animal to rest its emission system regularly.

Future Areas of Inquiry

Although the physical and structural aspects of dolphin echolocation clicks are well researched, knowledge of how dolphins use this sense in the wild is at its infancy.

Critical areas for future research described in other chapters in this volume include (1) measurement of echolocation signals, especially high-frequency clicks, in free-ranging dolphins (Schotten et al., chapter 54; Lammers et al., chapter 58); (2) social and nonsocial uses of echolocation both in captivity (Blomquist and Amundin, chapter 60; Moreno, Kamminga, and Stuart, chapter 59)

and in the wild (Herzing, chapter 56); (3) signal propagation (Watkins and Daher, chapter 57); passive versus active use (dos Santos and Almada, chapter 55); and (4) cross-modal studies of echolocation (Pack, Herman, and Hoffman-Kuhnt, chapter 41). Continued research is needed in these areas to ensure the future understanding of the function of dolphin echolocation in the wild.