# Dolphin Biosonar Echolocation
# A Case Study

**by**
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**(Appendix L on the website)**

***Structure without function is a corpse;***
***function without structure is a ghost***
Vogel & Wainwright, '69

## 1.0 A case study in echolocation and communications in the dolphin

**A Table of Contents and an Index are available at the end of this Appendix.**

Ketten has provided a broad overview of the marine mammal ear that supports this analysis, except it is archaic with regard to the connection between the peribulla region containing the cochlea and the external ears of these animals adjacent to the lower mandible[1].

The order *Cetacea* (whales, porpoises and dolphins) is well known for its broad use of its unique underwater capability in active echolocation and communications. The capability appears to be particularly well developed in the dolphin, suborder *Odontoceti*, and particularly in the genus *Tursiops* of dolphins. This study will focus on the most carefully studied member of this genus, the well-known bottlenose dolphin, *Tursiops truncatus*[2].

Taxonomy
Kingdom: *Animalia*
Phylum: *Chordata*
Class: *Mammalia*
Order: *Cetacea*
Sub-Order *Odontoceti*
Family: *Delphinidae*
Genus: *Tursiops*
Species: *truncatus*

The echolocation capability of the smaller, spinner, spotted or striped dolphins, *Delphinidae Stenella* appears to be significantly less than for *Tursiops truncatus*. Hemilia et al. has studied the middle ear

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[1]Ketten, D. (1990) The marine mammal ear: specializations for aquatic audition and echolocation *In* Webster, D. Fay, R. & Popper, A. *eds*. The Evolutionary Biology of Hearing. NY: Springer Chapter 35

[2]http://www.nmfs.noaa.gov/pr/species/mammals/cetaceans/bottlenosedolphin.htm

of the Sub-Order *Odontoceti*[3]. Interestingly, their model of the middle ear of this Sub-Order did not fit the performance data of the bottle-nosed dolphin, *Tursiops truncatus*. This finding supports the position taken here that the echolocating members of Odontoceti have evolved significantly with respect to hearing compared to other members of the toothed whale Sub-Order. Hemila et al. did not perform any laboratory investigations. They did not offer a graphic representation of their mathematical model. Their scaling procedures appear suspect.

Au has noted[4], "The use of acoustic energy is probably the most effective way to probe an underwater environment for purposes of navigation, obstacle avoidance, prey and predator detection and object localization and detection." It also appears optimum for intraspecies communications and intraspecies peer tracking.

Much of the material on the neural system in this study is drawn from a much more comprehensive treatise on hearing available on the Internet, "Processes in Biological Hearing," at www.hearingresearch.net. That material is voluminous. A guide to that material is to be published during 2007 as "Biological Hearing: A 21st Century Tutorial." The above website will highlight the publication and availability of the guide. Paragraph numbers shown below in square brackets refer to paragraphs in the downloadable chapters on the website (ca. 2006).

## 1.1 Overview of hearing and active echolocation in Dolphins

Dolphins rely upon their active and passive sonar capabilities for their livelihood. Consequently, the performance of these systems is highly developed, and probably near optimum in performance. The acoustic capabilities of the dolphins have been studied extensively (partly because of their military potential and their ability to influence military hardware design). However, Cranford made an important statement in 2000. "Our current understanding of aquatic echolocation by *odontocetes*, especially in free-ranging animals, is in its infancy."

A review of the unclassified literature suggests the field has not employed a system analyst in support of the extensive past empirical programs. The current literature is polarized as to the overall acoustic capability of the dolphins. One camp supports a capability with the larynx as the acoustic source. Another supports a capability that deprecates the larynx as a source. Morris has provided an overview of this controversy as of 1986[5].

A system analyst, without an in-depth review, would immediately suggest that the dolphin probably uses both capabilities. It would use the lower frequency whistles for long range, and possibly Doppler discrimination, due to the lower attenuation of water in that frequency region. Alternately, it would use higher frequency clicks for accuracy, particularly in angular spatial resolution, where range was not an issue. It would seem unusual for the dolphin to give up the low frequency echo detection capability that it brought with it from its terrestrial days. Even humans can make crude range estimates by yelling in a rock canyon and estimating the time the echo is heard.

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[3]Hemila, S. Nummela, S. & Reuter, T. (2001) Modeling whale audiograms: effects of bone mass on high-frequency hearing *Hear Res* vol 151 pp 221-226

[4]Au, W. (1989) Target detection in noise by echolocating dolphins *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pp 203-216

[5]Morris, R. (1986) The acoustic faculty of dolphins *In* Bryden, M. & Harrison, R. *eds*. Research on Dolphins. Oxford: Clarendon Press chap 18

From a system design perspective, the biosonar of the bottlenose dolphin, *Triosops truncatus*, is probably the most sophisticated target location and analysis system in existence. It at least equals the performance of the most advanced military sonars and radars. The sonar of the bottlenose dolphin can be described as a multifunction, multifrequency, multimode, physically adaptable monopulse sonar with extensive pattern matching capability and optimal interference rejection. In addition, it offers both binaural receiving and biphonic (or bivocal) transmitting capabilities. As a result, the dolphin has a short range echolocation and analysis capability at less than 100 meters that is not matched by any man-made system. Within the range of 100 to 600 meters, the dolphin has a highly optimized system tailored to its particular ecological niche, and not necessarily comparable to any man-made system. The dolphin apparently has no need for echolocation beyond 600 meters. It may have a need for communications (and potentially direction finding) at ranges greater than 600 meters.

The features described above for the bottlenose dolphin are packaged within a volume of one cubic foot and offers all of the features of the Ku band radar on the Shuttle space transportation system. As in the case of the Shuttle, the dolphin echolocation system can also be used for intra-species communications. The system is used for this function so extensively, and their repertoire of signals is so wide, the dolphins are sometimes described as "sea canaries" like their better known cousins the Beluga whales.

This analysis explores the anatomy, morphology, physiology and performance of the system of the bottlenose dolphin in considerable detail.

The controversy over the larynx versus the upper nasal passages as a high frequency acoustic source (frequencies greater than 30 kHz) was not resolved in a comprehensive analytical manner until the introduction of high speed X-ray and MRI techniques in the 1990's. The resolution was dramatic and showed that most of the descriptive material in the *Cetacea* literature prior to 1990 must be discounted.

Recent statements by Au[6], quoted in Abawi, et. al., appear to reflect the lack of an overall system analysis of the acoustic capabilities of the dolphin. "Despite their impressive performance, the dolphin's reception and transmission subsystems are quite mediocre compared to its signal processing capabilities[7]." On its face, this statement appears to reinforce the timeliness of Professor Norris's position; "One fact has consistently emerged from recent biological studies, particularly in the spheres of biophysics and anatomy, and it is that we humans have, in the past, usually underestimated the refinements of animal adaptation. Accordingly, if we are to establish a working hypothesis for cetacean echolocation and its anatomical correlates, it is probably better to expect sophistication . . . " (Norris 1964, p. 324).

From an analyst's perspective, the literature suggests a much more capable reception and transmission system than many perceive. It is also important to appreciate that the signal processing system can only process information received from the reception and transmission systems. The sonar of the bottlenose dolphin is considerably more sophisticated than any current

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[6]Au, W. (2004) The dolphin sonar: excellent capabilities in spite of some mediocre properties *In* Porter, M. Siderius, M. & Kuperman, W. *eds*. High Frequency Ocean Acoustics. Melville, NY: AIP Conference Proceedings

[7]Abawi, A. Hursky, P. Porter, M. et al (2004) Biomimetic signal processing using the biosonar measurement tool (BMT) *In* Porter, M. Siderius, M. & Kuperman, W. *eds*. High Frequency Ocean Acoustics. Melville, NY: AIP Conference Proceedings pp 260-271

man-made sonar in the world. It rivals the most advanced airborne radars available today. Merely listing the most obvious properties of this biological sonar (biosonar) attests to its fantastic capabilities. It is fundamentally a multi-band, multi-mode (including Doppler detection) frequency-hopping, steerable beam, binaural receiver, camouflage penetrating, single-pulse (when required) system with properties at least as sophisticated as the latest stealth fighter plane, the F-117, and latest stealth bomber, the B-2. The system is also multi-application, serving as both a sonar system and an intra-species communications system, like the Ku-band radar of the Space Shuttle.

This paper will surface a variety of system features that support the above description of the combined transmission, reception and data processing systems of the bottlenose dolphin in particular. Many of these features were only suggested obliquely in the literature prior to the year 2000.

A major problem in discussing the functionality and capability of the dolphin's hearing is the extremely small number of animals that have been studied. In many cases, sweeping conclusions have been drawn by investigators working with a single animal. Averaging of data, related to any parameter, from more than five specimens is a rarity. As shown in some of the graphs of Norris, et al, the variation in a parameter can approach twice the mean[8]. In such cases, the data is as representative of a dichotomy as it is representative of a Gaussian variable. In the case cited, the types of sounds produced by eight specimens were examined.

Because of the few specimens examined by any individual investigator, the description of the morphology, physiology and performance of the species presented here will necessarily be tentative.

A major point regarding echolocation in marine mammals relates to the method of range detection. Man-made sonar machines rely heavily upon measuring the time of travel of a pulse to determine the absolute range to a target. The times to be measured are on the order of microseconds and require circuit bandwidths greater than 100,000 Hz. High stability oscillators (at least a few parts in $10^8$), and complex counters are *de rigueur,* and an absolute range is required so its value can be communicated to some other human at a distance. Known mammalian biology does not support circuit bandwidths greater than 1000 Hz. Because of this great discrepancy, the investigator should focus on other methods of range determination in *Cetacea.* A method that overcomes the neurological bandwidth limit is the use of phase locking in a "servomechanism loop." The oscillation used as a reference in this servo loop provides a relative indication of distance to the target without using any high frequency oscillators, counters or other circuits of Man's technical toolbox. A relative range is all that is needed by an autonomous biological system.

Based on the above brief discussion, the following should be noted. Cetaceans do not use precision time measurement techniques in ranging and, like other mammals, they do not use transcendental calculations in angle measurements.

### 1.1.1 Species specific background

As a brief aside, the vision of the dolphin has not been investigated at a detailed level and the literature contains a variety of anecdotal comments. There are frequent assertions that the dolphin

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[8]Norris, K. Wursig, B. Wells R. & Wursig, M. (1994) The Hawaiian Spinner Dolphin, Berkeley, Ca: University of California Press pg 169

is nearsighted out of water, in analogy to the human being farsighted in water (Reynolds, p. 81)[9]. The analogy is questionable because the dolphin does not depend on its cornea for a major part of the optical power of its visual imaging system. The outer cornea is nearly flat and of constant thickness except at the very edges. Caldwell & Caldwell (pg 107) insist on the excellent vision of the dolphin out of water. They illustrate this by showing a dolphin leaping more than 6 meters into the air to snatch a small fish from the teeth of a performer at an aquarium. A scenario in Ridgway suggests a dolphin may recognize a specific person at about 20 meters using either vision or hearing in air[10]. It is noted that the two eyes of the dolphin, which are located on opposite sides of the head, do rotate independently. The dolphin appears to have some forward (binocular) vision but it appears to be limited. It may or may not involve a fovea as in many other mammalian species. Nachtigall, et. al. provided the best description of dolphin vision up to 1986[11]. Ridgeway & Carder and later papers in that volume provide a variety of useful acoustic parameters (some related to the baluga whale). The inconsistency in the available data is obvious in those papers. Supin, et. al. provided a much better description in 2001[12]. It shows specifically how the bottlenose dolphin eye has evolved differently than the human eye and is uniquely designed to maintain proper focus whether in or out of the water.

### 1.1.1.1 Literature

Ridgway & Harrison have provided a two volume set of data concerning dolphins in handbook form[13]. Barnes, in Chapter 1 of Leatherwood & Reeves, reviews the phylogeny of order *Cetacea* (whales, dolphins, and porpoises) and the evolutionary sequence of changes related to the dolphins of the family *Tursiops* in particular[14]. It appears these mammals left land between 70 and 90 million years ago. The dolphins are members of the suborder *Odontoceti* (whales that possess at least one row of teeth as adults). There are four super families within *Odontoceti*; including the largest, *Delphinoidea*. *Delphinoidea* includes the *Tursiops* family. *Cetacea* are most closely related to the hippopotamus and other ruminants having multiple stomach chambers. The dolphins swallow their food whole. Heyning & Mead have provided additional details relative to the evolution of the nasal structures of *Cetacea*[15].

Ridgway, in Chapter 4 of Leatherwood & Reeves, reviews the morphological features of the brain and central nervous system of the bottlenose dolphin, *Tursiops truncatus*. Truncatus refers to the significant wearing of the teeth in adulthood. He makes a number of comparisons with the brain of

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[9]Reynolds III, J. Wells, R. & Eide, S. (2000) The Bottlenose Dolphin. Gainesville, FL: University Press of Florida

[10]Ridgway, S. (1995) Dolphin Doctor, 2nd Ed. San Diego, Calif: Dolphin Science Press pg 81

[11]Nachtigall, P. (1986) Vision, audition, and chemoreception in dolphins and other marine mammals *In* Schusterman, R. Thomas, J. & Wood, F. *eds*. Dolphin Cognition and Behavior: A Comparative Approach. Hillsdale, NJ: Lawrence Erlbaum Associates Chapter 4

[12]Supin, A. Popov, V. & Mass, A. (2001) The Sensory Physiology of Aquatic Mammals. Boston, MA: Kluwer Academic Publishers Chapter 4

[13]Ridgway, S. & Harrison, R. (1981) Handbook of Marine Mammals, Vols 5 & 6. NY: Academic Press

[14]Barnes, L. (1990) Fossil record and evolutionary relationships *In* Leatherwood, S. & Reeves, R. *eds*. The Bottlenose Dolphin. NY: Academic Press pg 10

[15]Heyning, J. & Mead, J. (1989) Evolution of the nasal anatomy of *Cetaceans In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pp 67-79

humans, which it is of comparable brain weight to total weight. He notes that, contrary to the human literature, the brain of the dolphin is clearly more convoluted than that of humans. With regard to the auditory system, Ridgway references Bullock & Gurevich. They note the size of the medial geniculate is about seven times that in humans, the inferior colliculus is about 12 times its human analog, and the nucleus of the lateral lemniscus is more than 250 times as large as the equivalent structures in humans. The ventral cochlear nucleus is also massive compared to the human analog. The auditory nerves are similarly larger than in comparable humans (70,000 to 100,000 neurons with mean diameters of 12 microns[16]). The visual system, on the other hand is less well developed in these animals with no obvious fovea centralis. Because of packaging changes, the location of activity on the cerebral cortex appears significantly different from in humans. The analog of layer four (the granular layer) of the human cortex is absent or difficult to locate in the dolphin brain.

The detailed character of the sound generation and sound receiving systems of the dolphin, and *Cetacea* in general, remain poorly documented. Morris provides a comprehensive listing of the features of these systems (in 1986) interpreted by two different schools (the American and the European, p. 380-381) and resulting in two widely differing opinions of how the echolocation system in dolphins operates[17]. The interpretations were far from compatible in 1986. He addresses this dichotomy finally on page 393. Morris closed with a comment concerning the slowness of future progress in observing the dolphin in their natural habitat unless some new and unexpected techniques should arise. The recent development and use of self-contained, GPS-based, navigational recording and reporting capabilities along with new miniaturized acoustic data recording capabilities appear to have solved this problem.

The literature notes the asymmetries in both the overall configuration of the forward torso of the dolphin and specifically in the melon within the forehead area (Au, p. 89). This appears to be similar to the asymmetry found in the outer ears of owls, and possibly bats. However, in the case of the dolphin the asymmetry is in the transmitting mechanism instead of the receiving mechanism. In both cases, the asymmetry probably introduces a vernier into the spatial location determination. A slight vertical motion of the head introduces a slight horizontal change in the predicted target location. Cranford, Amundin & Norris provide the broadest possible analysis of the anatomy of the Odontocete related to sound generation. They used a variety of X-ray tomography, MRI, and various histological techniques to study 40 specimens from 19 species[18]. An asymmetry in the ultra high frequency energy generating system is also noted. The material is extremely useful but their proposals relating to the mechanism of sound generation are only first-order. Cranford has described the right-hand energy generator, within the right nare, as being twice the size of the left-hand generator[19].

The asymmetry in the dolphin head is much smaller than the amount of space given to the subject in

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[16]Supin, A. Popov, V. & Mass, A. (2001) The Sensory Physiology of Aquatic Mammals. Boston, MA: Kluwer Academic Publishers pg 25

[17]Morris, R. (1986) The acoustic faculty of dolphins *In* Bryden, M. & Harrison, R. *eds*. Research on Dolphins. Oxford: Clarendon Press Chap 18

[18]Cranford, T. Amundin, M. & Norris, K. (1996) Functional morphology and homology in the odontocete nasal complex: Implications for sound generation *J Morphol* vol 228, pp 223-285

[19]Cranford, T. (2000) In search of impulse sound sources in *Odontocetes In* Au, W. Popper, A. & Fay, R. *eds*. Hearing by Whales and Dolphins. NY: Springer Chapter 3, pg 134

the literature. Houser, et. al. have provided imagery and a discussion supporting this point[20]. The asymmetry is perceptible but not obvious to the non-anatomist.

Caldwell, et al. have provided a good review of the low frequency signaling by the bottlenose dolphin[21]. The purpose of these whistles has not been adequately described. Caldwell et al. described distress and signature whistles that suggest communications. She also describes concern whistles associated with a change in depth of the water in its enclosure. While these whistles can be considered distress calls, they can also be considered investigative whistles, re-measuring the available size of the enclosure. Ridgway has documented even clearer examples of dolphin communications, both through water and through air[22]. The vision of the dolphin is comparable to that of the human (recognizing an individual person from several hundred feet away).

The Ridgway book was prepared for the popular press. However, it contains many interesting physiological facts about the bottlenose dolphin. These facts include:

- comments on communications and sound imaging on pages 56-61 & 87,
- maximum diving depths exceeding 1000 ft on page 11,
- maximum speeds on the order of 25 miles per hour (40 kilometers per hour) on page 70,
- maximum heart rates of 100 beats per minute after deep diving or maximum exertion,
- resting heart rates of 35 beats per minute on page 97,
- typical respiration interval of 30 seconds but it can hold its breath for up to four minutes,
- oxygen level in lungs reduced to 2% after three minutes and,
- excellent vision in air (identifying humans at several hundred feet distance) on page 80.

A team including Ridgway produced two important papers in 1980 on the musculature in the head of the dolphin and the pressures within the passageways during phonation[23,24]. The data describing the sounds produced during testing is less complete.

Au has presented a wealth of information on the high frequency capability of the combined aural and hearing systems of the dolphin *Tursiops truncatus*, and other *odontocetes*[25]. The high frequency signals are dominated by short clicks.

Hughes has presented a popular press oriented book on echolocation and other exotic sensory

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[20]Houser, D. Finneran, J. et al. (2004) Structural and functional imaging of bottlenose dolphin (Tursiops truncatus) cranial anatomy *J Exp Biol* vol 207, pp 3657-3665

[21]Caldwell, M. Caldwell, D. & Tyack, P. (1990) Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin *In* Leatherwood, S. & Reeves, R. *eds*. The Bottlenose Dolphin NY: Academic Press Chap 10

[22]Ridgeway, S. (1995) Dolphin Doctor, 2nd Ed. San Diego, CA: Dolphin Science Press pg 51

[23]Green, R. Ridgway, S. & Evans, W. (1980) Functional descriptive anatomy of the bottlenose dolphin nasolaryngeal system *In* Busnel, R-G. & Fish, J. eds. Animal Sonar Systems NY: Plenum Publishing pgs 199-238

[24]Ridgway, S. Carder, D. Green, R. et. al. (1980) Electromyographic and pressure events in the nasolaryngeal system of dolphins during sound production *In* Busnel, R-G. & Fish, J. eds. Animal Sonar Systems NY: Plenum Publishing pgs 239-249

[25]Au, W. (1993) The Sonar of Dolphins. NY: Springer-Verlag

modalities[26]. While citing both Au and Ridgeway with regard to the dolphins, it is superficial and does not introduce the continuous wave signals of the dolphin. It is written by a non-specialist and develops a conjectural framework based on his reading. It addresses echolocation in the mustached bat from a similar perspective and approach. In that application, he does develop the concept of a variable frequency signal source to keep the Doppler shifted echo within a narrow frequency range for which the cochlea is optimized.

Currently, the definitive description of the morphology of the bottlenose dolphin is that of Cranford, Amundin & Norris of 1996[27]. It is based on *in-vivo* CT and MRI scanning. The report is extensive, figures are well annotated, supported by an extensive bibliography, provides tabular values for many elements and contains many figures in color. The goal of the study was to provide quantitative data on the size, shape, degree of asymmetry and geometric configuration for the components of the impulse sound generation mechanism in the odontocete forehead. They provide a concise discussion of the terminology found in the literature. Although the authors indicate they collected data on a large number of specimens (~40 representing 19 species), the number for any one species is quite small. In addition, they note that they do not have both morphology data and sound recordings from the same animal.

Unfortunately, when they begin to discuss the physiology of the various members of Cetacea based on their data, they limit the discussion to click generation (as opposed to continuous tone and other potentially communications-oriented sounds).

Au presented an unusual paper in 2004[28]. It described the signal generation and signal receiving capabilities of the dolphin as mediocre on three occasions without providing a detailed description of the actual capability of the species. This work suggests that the capabilities are, on the contrary, quite sophisticated. Au made two observations in his discussion section. "However, within a 100 m range, there is not a technological sonar that can rival the dolphin in discriminating and recognizing targets." He continued later. ". . .and, we should strive to produce a short-range sonar system that can perform as well as the dolphin." This work suggests much of that capability is due to the sophisticated signal generation and signal receiving capabilities of the dolphin, in addition to its signal processing and cognitive abilities. Floyd, a colleague of Au, has shown that the figure of merit frequently used to evaluate man-made sonars does not give a rational value for the dolphin[29]. A careful reading of Floyd's paper shows his performance estimates are not based on the physiology of the dolphin, particularly its associative correlation capabilities, but on estimates based on simple techniques used in common man-made sonar systems (See also **Section 1.5**). He does note, the wideband echolocation signal (apparently pulse mode) and binaural receivers "provides for superior target recognition capabilities, better target detection in reverberation, and far better spatial resolution than conventional sonars with similar beam widths."

Au's computation of the equivalency between a long constant amplitude tone burst and the shaped

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[26]Hughes, H. (1999) Sensory Exotica. Cambridge, MA: MIT Press

[27]Cranford, T. Amundin, M. & Norris, K. (1996) Functional morphology and homology in the odontocete nasal complex: implications for sound generation *J Morph* vol 228, pp 223-285

[28]Au, W. (2004) The dolphin sonar: excellent capabilities in spite of some mediocre properties *In* Porter, M. Siderius, M. & Kuperman, W. *eds*. High Frequency Ocean Acoustics. Melville, NY: Amer Inst Physics

[29]Floyd, R. (1986) Biosonar signal processing applications *In* Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pg 774

tone burst of the pulse-based dolphin system appears irrelevant. While the energy in the longer burst is obviously higher, and its detectability at longer ranges would be higher, other performance aspects of the dolphin system would be seriously compromised by the use of such a long burst.

Au provides some critical band measurements from Lemonds, et. al[30]. These measurements do not represent the minimum frequency difference sensitivity of the dolphin. It can be shown they represent the equivalent noise bandwidth of the multidimensional correlator of the dolphin PGN (Section 1.4.4). The minimum detectable frequency difference is much narrower than the critical band value (Section 1.4.2.4.2).

Cranford has recently provided a chronologic look at the quest to understand the biosonar system of marine mammals[31].

### 1.1.1.2 Brief Glossary

As Cranford, Amundin & Norris note on page 224, "In the fusiform cetacean body architecture, posterior is synonymous with caudal, anterior is synonymous with rostral, dorsal is synonymous with superior, and ventral is synonymous with inferior." They also note that many terms have entered the lexicon of Cetacea that were not developed by anatomists. A brief list of terms important to this study is summarized below. A few of these terms have meanings unique to this study.

**Ablaut**– The Proto-Indo-European system of root vowel alternations.

**Allophone**– The different sounds that can represent one phoneme in the speech of a given speaker or language; that is, they are perceived under certain circumstances to be the same phoneme. Allophonic systems can vary from speaker to speaker or more especially from language to language. e.g., /s/ can be represented by the allophones /s/ and /z/ (sound or sounds).

**Articulation**– The point of production of the various segments in the oral cavity.

**Biosonar**– A biologically based system of sound source location by determining its angle and range. The system may be passive or active.

**Bound morpheme**– A morpheme which never occurs alone, but is attached to other morphemes. e.g., Eng. kindness, unlikely, Ger. Mädchen, inflectional endings, etc.

**Bursae**– A sac or sac like body cavity, especially one containing a viscous material. The material may constitute a liquid crystal and exhibit significant structure in its acoustic role.

**Commissure**– Used in two contexts in anatomy.

1. A tract of nerve fibers passing from one side to the other of the spinal cord or brain.
2. The point or surface where two parts, such as the eyelids, lips, or cardiac valves, join or form a connection.

**Consonant**– Any segment produced by stopping and releasing the air stream (stops), or stopping it

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[30]Lemonds, D. Au, W. Nachtigall, P. Roitblat, H. & Vlachos, S. (2000) High frequency auditory filter shapes in an Atlantic bottlenose dolphin *J Acoust Soc Am* vol 108, pg 2614(A)

[31]Cranford, T. (2000) In search of impulse sound sources in Odontocetes *In* Au, W. Popper, A. & Fay, R. *eds*. Hearing by Whales and Dolphins. NY: Springer Chapter 3

at one point while it escapes at another (liquids), or a very narrow passage causing friction (fricatives).

**CT**– Primarily X-ray based computed tomography. See tomography.

**Dialect**– 1. A regional variety of a language distinguished by pronunciation, grammar, or vocabulary, especially a variety of speech differing from the standard literary language or speech pattern of the culture in which it exists.
2. A language considered as part of a larger family of languages or a linguistic branch: Spanish and French are Romance dialects.

**Diphthong**– Syllabics which show a marked glide from one vowel to another, usually a steady vowel plus a glide. e.g., /ou/ in house, /oi/ in toy.

**Fricative**– A consonant produced when the air released by an articulator passes through a narrow passage with audible friction. e.g., [f], [s], [þ], [ð], etc.

**Globular bushy cells**– A morphological designation for the stage three signal encoding neurons in the ventral cochlear nucleus (VCN). Used in Zook & DiCaprio, 1990.

**Gular**– The throat.

**Junk**– A description (from the whaling industry) of the massive fatty tissue within the forehead of Cetacea.

**Language**– 1.The use of acoustic sounds in organized combinations and patterns in order to express and communicate thoughts and feelings.

2. An organized set of combinations and patterns of acoustic sounds used by a specific population to communicate thoughts and feelings.

**Lexicon**– *Linguistics*. The morphemes of a language (or dialect) considered as a group.

**Liquid crystal**– A unique state of matter that exhibits zero long term resistance to an applied pressure (will flow to fill a container) but can exhibit significant impedance to short term distorting forces. Such materials were frequently described as gels in the earlier literature.

**MLDB**–

**Magnetic Resonance Imaging (MRI)**– A method of stimulating individual molecules, causing them to vibrate at their molecular frequency, and recording (imaging) their density at a given location based on that vibration.

**Melon**– A description (in the vernacular) of the massive fatty tissue within the forehead of Cetacea.

**Monkey lips**– (a.k.a. phonic lips) A description (in the vernacular) of the valvular flaps located in each nasal passage within the head of *Cetacea*. Apparently capable of generating both fricative sounds and impulses by slapping the lips together.

**Morpheme**– The smallest unit of meaning. Any word or part of a word that conveys meaning and cannot be further divided into smaller meaningful elements.

**Morphology**– The study of forms of language, especially the different forms used in declensions, conjugations, and wordbuilding.

**Phoneme**– The simplest significant unit of sound. A phoneme may also have various allophones.

**Phonetics**– A branch of linguistics dealing with the analysis, description, and classification of speech sounds, or segments.

**Phonology**– The branch of linguistics concerned with the structural relationships between segments. The study of phonetics and phonemics together in the evolution of speech sounds.

**Pidgin**– A term used by linguists to define the first few words developed by two people seeking to converse but not speaking a common language.

**Principal call** A morphological designation for the stage three signal decoding neurons in the medial nucleus of the trapezoidal body (MNTB). Used in Zook & DiCaprio, 1990.

**Sac**– A pouch or pouch-like structure, sometimes filled with fluid or air. See theca.

**Theca**– A case, covering, or sheath holding something other than air. See Sac.

**Tomography**– A method of preparing detailed images of a predetermined plane section of a solid object while blurring out the images of other planes.

**Unvoiced**– A segment produced without any accompanying vibration of the vocal cords. e.g., [p] v. [b], or [t] v. [d], etc.

**Voiced**– A segment produced with accompanying vibration of the vocal cords. e.g., [b] v. [p], or [d] v. [t], etc.

**Vowel**– A voiced segment characterized by generalized friction of the air passing in a continuous stream through the pharynx and opened mouth, with relatively no narrowing or other obstruction of the speech organs.

### 1.1.1.3 Technical environment

#### 1.1.1.3.1 The acoustic environment of sea mammals

The acoustic sea environment is very complex and difficult to quantify. Both surface conditions and bottom conditions have a significant impact on sound reception within the sea environment. Within the volume of the sea, there are also many inhomogeneous features which can scatter sound. Simultaneously, the attenuation of sea water increases with frequency. As a result, most ocean communications are short range. An exception may be the very low frequency signaling (at frequencies below one kilohertz) between whales at considerable distance from each other. The signaling rate at such low frequencies is necessarily very low.

Tolstoy & Clay have described both the attenuation and noise environments in the sea[32]. **Figure 1.1.1-1** reproduces their figure 1.1 with extrapolations applicable to the dolphin. The major variation in attenuation, and the two-way attenuation inherent in echolocation, suggests the higher frequency ranges ( 80-150 kHz) are only available for short range echolocation (less than 100 meters). These ranges would probably be used only for precision ranging during predation. The range from 30-80 kHz offers greater range for the same peak source power at proportionately less resolution. It remains to be documented as to whether this frequency range is or is not associated with the range capability of 600 meters described above. The lower frequencies (200-1000 Hz) appear better suited for long range communications (such as across a large estuary). The communications source need only be strong enough to provide adequate signal strength at the receiver by overcoming the one-way attenuation. As noted above, frequencies below 200 Hz are thought to be used by the large whales to achieve very long range communications.

This figure can be extended to even lower frequencies to show why the larger members of Cetacea apparently use frequencies below 50 Hz to signal over intercontinental distances (although such signaling may also require the use of ducts within the ocean layers to avoid the uncontrollable spreading of the energy in undesired directions).

[32]Tolstoy, I. & Clay, C. (1966) Ocean Acoustics. NY: McGraw-Hill

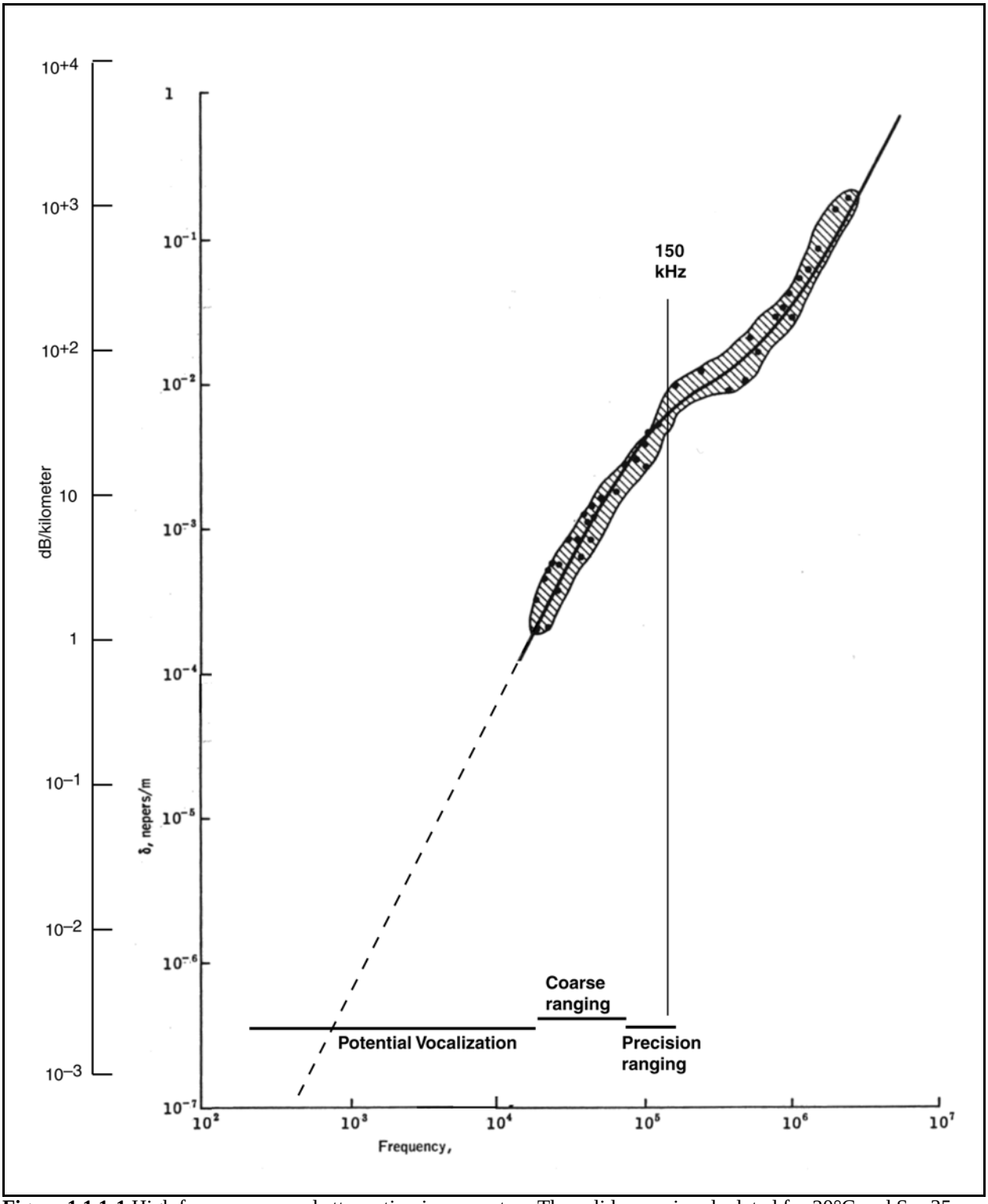


**Figure 1.1.1-1** High frequency sound attenuation in sea water. The solid curve is calculated for 20°C and S = 35 parts per thousand. Shaded area indicates experimental verification. The dashed curve and acoustic ranges are extrapolations by Fulton. 1 neper = 8.686 dB. Modified from Tolstoy & Clay, 1966.

Figure 1.4 of Tolstoy & Clay, on the noise environment, requires too much interpretation to reproduce here. However, Au has provided a graphic that is more direct. It clearly shows the noise spectrum as a function of acoustic frequency due to both animate and inanimate causes. Au noted the extremely high noise in Kaneohe Bay is due to the high concentration of snapping shrimp.

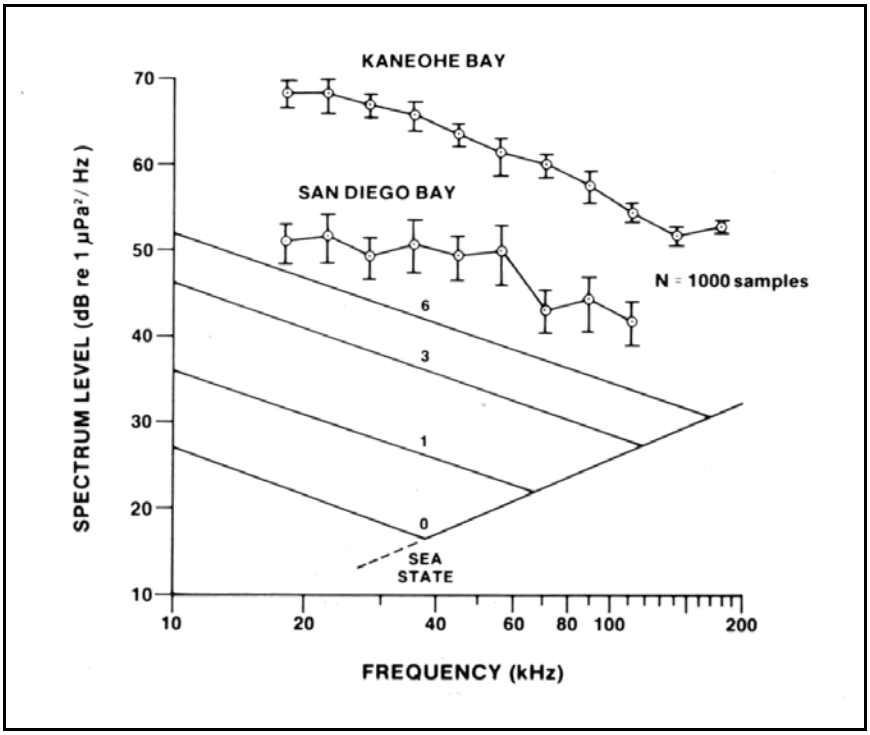


**Figure 1.1.1-2** Ambient noise in the ocean measured in 1/3 octave bands. Deep water noise for different sea states are shown for comparison. From Au, 1989.

### 1.1.1.3.2 The frequency range of dolphin emissions

The research community has not yet settled on a uniform description of the phonations of dolphins. Cranford has discussed this difficulty (p. 117). This work will use the following terms:

1. Low frequency (LF)– Signals generated in the pneumatic arena (larynx) and audibly detectable by humans without instrumentation. Typically in the frequency range of 200–15,000 Hz.

2. High frequency (HF)– Signals generated in the pneumatic or non-pneumatic arena (tissue and bones) by the larynx and propagated primarily in the aquatic environment. Typically in the 4,000–30,000 Hz frequency range.

3. Ultra high frequency (UHF)– Signals generated primarily in the non-pneumatic arena by the phonic lips (valvular flaps) and propagated exclusively in the aquatic arena. Typically in the 30-150 kHz frequency range.

This categorization separates the largely incidental pneumatically propagated LF sounds of the dolphin from its more significant HF and UHF sounds associated with echolocation. However, more recent investigations with more modern equipment suggests the HF region may extend up to at least 96 kHz.

The signals generated by the dolphin lips in the UHF are generally sinusoidal as expected by the ringing caused by the clapping together of two hard objects. The HF and LF spectrums show much broader ranges of frequencies simultaneously (that may or may not be harmonically related).

### 1.1.1.3.3 The dispersion of water-based liquids

The dispersion observed in sea water has had a checkered history. Herzfeld & Litovitz wrote a definitive work in the subject in 1959, even discussing the potential for water to form molecules more complex than $H_2O$[33]. While significant dispersion was reported in a number of papers immediately after World War II, Herzfeld & Litovitz disparaged these reports (page 354). They make a strong statement concerning pure water, i. e., water absent any dispersed solids (p. 428). "No velocity dispersion has been found." Herzfeld & Litovitz also described their experimental method of measuring the elusive (if present) parameter, dispersion, in a fluid (p. 365).

A review of the subsequent literature found very few comments concerning dispersion in sea water or fresh water. One exception is by Buckingham[34] who was studying sediment saturated water. Such a material is clearly a non-Newtonian fluid (**Section 4.1.4** in "Processes in Biological Hearing").

The literature suggests that dispersion is not a characteristic of concern in the propagation of sound in sea water, at least up to frequencies of 150 kHz.

### 1.1.1.3.4 Range and Range resolution in sea water

Weston has addressed sound propagation in the presence of bladder fish[35]. In brief, "in fish with bladders, the bladder volume approximates one-twentieth of its total volume. The gas in the bladder forms a very significant acoustic interface mismatch with the other tissue of the fish (with acoustic properties not significantly different than water. When present, the bladder dominates the acoustic scattering and absorbing properties of the fish at low frequencies and still plays a big part at higher frequencies." Of particular interest is the Q of the bladder-tissue combination. "For an ideal bubble at atmospheric pressure the Q is over 70, but experimental work suggests values of the order of 4 or 5 for fish." In calculating the Q, the spring factor is due to the low elastic modulus of the gas and the mass comes from the relatively high inertia of the surrounding tissue or water.

### 1.1.1.3.5 Range and Range resolution in sea water

**Figure 1.1.1-3** shows the round trip travel time for an acoustic pulse in sea water and the time difference resolution required to achieve a given range resolution. The maximum range of the bottlenose dolphin has been estimated from the maximum pulse interval commonly measured for its high frequency echolocation system. Morris reported this value as 0.6-0.8 seconds[36]. The maximum range of the ultra high resolution pulse echolocation system is on the order of 100 meters for a 7.62 cm diameter metallic test sphere[37].

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[33]Herzfeld, K. & Litovitz, T. (1959) Absorption and Dispersion of Ultrasonic Waves. NY: Academic Press

[34]Porter, M. Siderius, M. & Kuperman, W. *ed*. (2004) High Frequency Ocean Acoustics. NY: American Institute of Physics. Chapter 1.

[35]Weston, D. (1967) Sound propagation in the presence of bladder fish In Albers, V. ed. Underwater Acoustics Vol 2. NY: Plenum Press Chap 5

[36]Morris, R. (1986) The acoustic faculty of dolphins *In* Bryden, M. & Harrison, R. *eds*. Research on Dolphins. Oxford: Clarendon Press pg 388

[37]Au, W. (1989) Target detection in noise by echolocating dolphins *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press Pg 205

The range resolution of the ultra high frequency echolocation system of the bottlenose has remained controversial. Values as low as 1.5-4 mm (requiring a time difference resolution of 1-3 μsec) have been reported. Such a value would require much broader neural signaling circuits than normally found in mammals or exceptionally sophisticated signal manipulation within the neural system.

Au confirmed the range resolution of the bottlenose was unknown in 1993. When speaking of the ultra high frequency echolocation system, he suggested it was probably 12-15 μsec (1.0 to 1.1 cm)[38].

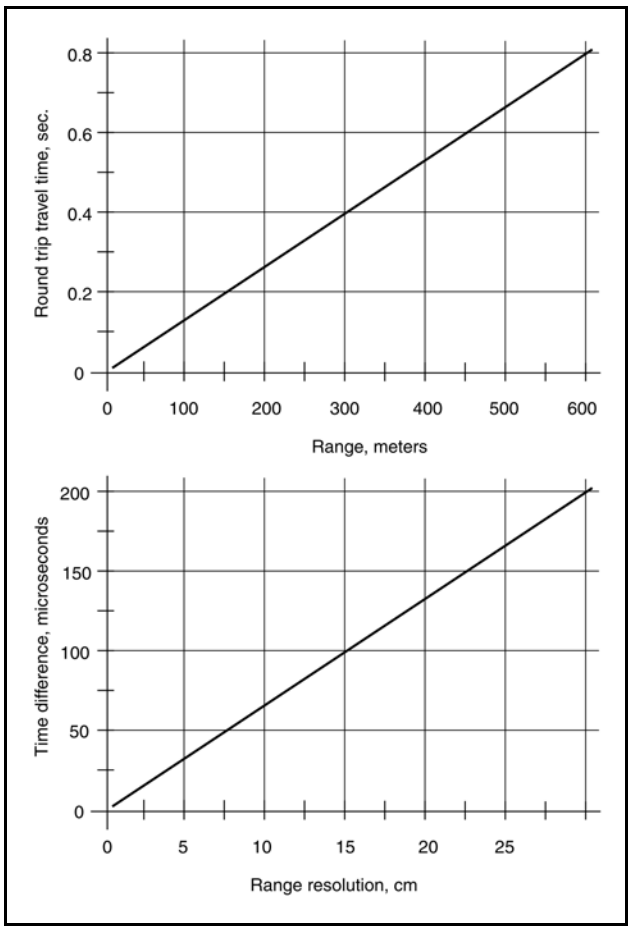


**Figure 1.1.1-3** Range equation and range resolution in sea water.

## 1.1.1.3.6 Doppler frequency versus velocity in sea water

It is likely that the Doppler frequency resulting from the motion of targets illuminated by the echolocation capability of dolphins plays an important role in their overall acoustic performance.
**Figure 1.1.1-4** provides the relationship between frequency shift and relative target velocity in sea water. A nominal maximum velocity for the dolphin is shown along with a preliminary estimate of the minimum velocity difference required by the echolocation system of a dolphin to detect a moving target. These estimates will be justified in the following discussion.

[38]Au, W. (1993) Op. Cit. pg 240

### 1.1.1.4 Echolocation in Humans

Recently, discussions have appeared concerning the ability of humans to use short range echolocation effectively. The Learning Channel recently presented a program, entitled "The Boy Who Sees through Sound," concerning Ben Underwood, a teenager blind since the age of three due to retinal cancers in both eyes. Beginning at that age, he began experimenting with clicks generated between his tongue and teeth with the goal of understanding his surrounding environment. Using this largely unobtrusive source, he is able to interrogate his environment within a forward hemisphere of about ten feet. At ranges of a few feet or less, he is able to differentiate rectangular objects from cylinders and sizes down to on the order of one inch.

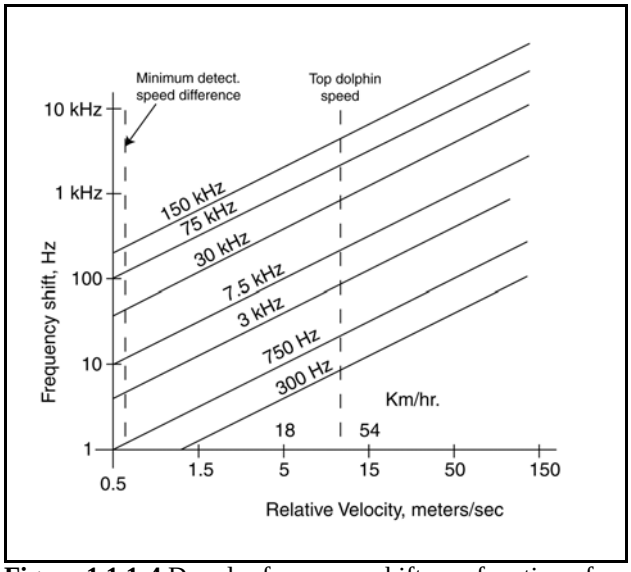


**Figure 1.1.1-4** Doppler frequency shift as a function of relative velocity in sea water.

Daniel Kish operates "World Access for the Blind." Google and Wikipedia are a good source for more information on this capability. The wavelengths of sound in air are about 3.5 times longer than those in water. The human auditory range is also limited to less than 15 kHz for practical purposes Therefore, the range and azimuth capabilities of human echolocation are considerably poorer than those of dolphins.

## 1.1.2 Overall vocal and auditory physiology of the dolphins

The literature of dolphin anatomy and physiology has been lacking in detail until 1995 or later. The advent of computer-aided tomography has led to rapid advances since that time, albeit based on only a few examinations. Houser et al. provides valuable anatomical data but little discussion of how the parts play together[39]. Recently, Mead & Fordyce have contributed a massive lexicon of the anatomical features of the cetacean skull[40].

The physiology of hearing in dolphins and other members of *Cetacea* is built on the generic mammalian vocal and auditory systems. However, significant modifications and extensions have been introduced into the system. A prominent reorganization of the overall sensory architecture has resulted in the introduction of a precision echolocation servo system (PES), or a precision echolocation servo loop, much like the precision optical servo loop of vision in the higher mammals. **Figure 1.1.2-1** illustrates these changes in block diagram form. The active echolocation system requires the close integration of the vocal system (nominally a stage 6 activity) and the auditory sensory system (stages 1-3), along with the expanded (stage 4a) signal manipulation capability, not involving the cerebral cortex, required to extract the additional information provided.

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[39]Houser, D. Finneran, J. Carder, D. et al. (2004) Structural and functional imaging of bottlenose dolphin (Tursiops truncatus) cranial anatomy *J Exp Biol* vol 207, pp 3657-3665

[40]Mead, J. & Fordyce, R. (2009) The Therian Skull: A Lexicon with Emphasis on the Odontocetes. Wash. DC: Smithsonian Institution Contributions to Zoology Number 627 SCtZ-0627.pdf

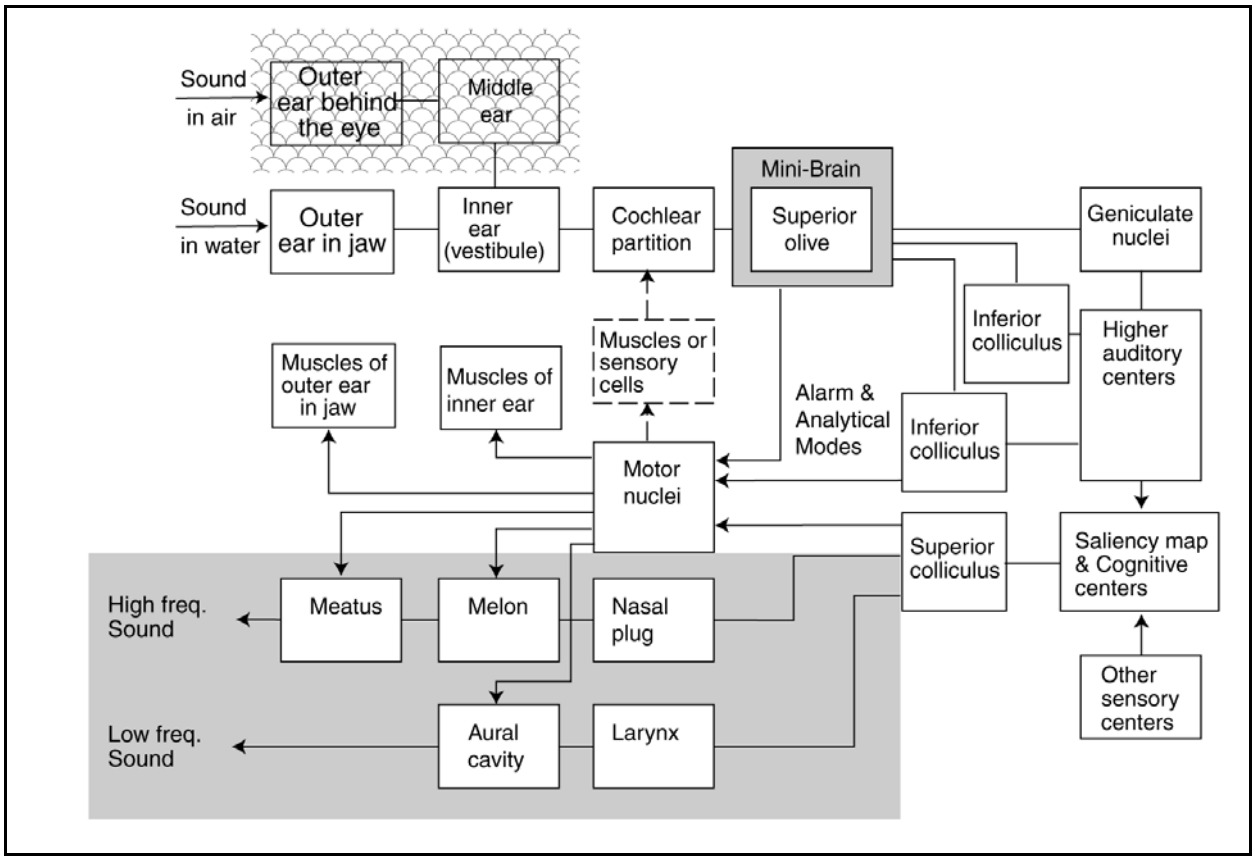


**Figure 1.1.2-1** Top level block diagram of vocal and auditory systems in dolphin. A new precision echolocation servo loop has been implemented by combining the active sound generation capability of the expanded vocal system (stage 6) with the wide frequency spectrum binaural auditory system (stages 0 through 4). The bones of the middle ear of terrestrial mammals are no longer functional in dolphins since impedance matching between air and water is no longer required.. The hatched area has atrophied in the Order *Cetacea.*

A major deletion involves the middle ear used by terrestrial chordates as an acoustic impedance matching device. It is not needed by animals who have returned to the marine environment exclusively. The small bones of the middle ear and the oval window have atrophied, and it is likely the tympanic membrane now serves as a barometric depth gauge. Energy from the outer ear formed by the outer skin and highly tailored fat tissue below and behind the lower jaw enters the vestibule of the labyrinth (called the .bulla in animals not relying upon an ornate vestibular system to establish their orientation) through a different thin wall of the vestibule as illustrated in **Figure 1.1.2-3**.

A different set of highly facile muscles are used to shape the outer surface and the inner fat tissue of the outer ear in order to optimize the pointing and beam forming capability of the outer ear.

Dolphins are known to produce a wide range of acoustic signals in conjunction with the above system. Reynolds, et al (page 76) have provided a simple table of dolphin sounds. **Table 1.1.1-1** provides an expanded table relating more functional parameters. A much more comprehensive description of

dolphin sounds is given by Herzing[41]. Even the Herzing description is light on the characteristics of signaling during echolocation and detailed target analysis. It does not address the physiology of signaling.

Two features of the dolphin not widely discussed are;

• The dolphins do not generate sound within their throat behind their mouth. Thus, they do not "speak" through their mouth but through their blow-hole.

•The dolphins do not receive sound energy through their "auditory canal." Thus, they do not hear through the ports on the side of their head that people associated with their ears. They hear exclusively through the underwater receivers located on each side of their heads below and behind their lower jaw.

### 1.1.2.1 Acoustic signals used by the dolphin

**Table 1.1.1-1**
**Acoustic signals processed by dolphins**

| Frequency Range | Sound Type | Active/Passive | Function |
|---|---|---|---|
| Coarse Long Range Capability | | | |
| 0.2–0.9 kHz | Phase coherent listening | Passive | Source Location |
| 4–20 kHz whistles | Spatially coherent reflections | Active | Location, Ranging, & Doppler velocity |
| 4-20 kHz barks, yelps, rasps | One way signaling | Active | Intra species communications |
| Fine Short Range Capability | | | |
| 30–150 kHz clicks | Spatially coherent reflections | Active | Location, Ranging & potential acoustic imaging |

The low frequency active system operates in a frequency range where the wavelength of the emitted sound is long with respect to the size of many food items. Furthermore, it is long with respect to the geometry of the vocal apparatus within the dolphin. The resulting system is not very directionally specific. The source energy is distributed nearly omnidirectionally but the binaural capability of the receiving system provides some directionality. It is used primarily for investigating the animals environment (distance to surface, bottom characteristics and distance) and detecting large objects or

[41]Herzing, D. (2000) Acoustics and social behavior of wild dolphins: Implications for a sound society In Au, W. Popper, A. & Fay, R. Op. Cit chapter 5

groups of objects. Similarly, the lowest frequency capability is limited primarily to the binaural reception of signals generated by external sources.

The high frequency active system operates in a range where the wavelength of the emitted sound is small relative to potential food items. As will be discussed below, it is quite possible the dolphin is able to create an acoustic image of individual targets within the narrow beam of its field of view at these frequencies.

Various authors have attempted to segregate the frequency spectrum of high frequency acoustics[42]. The division appears clear for the dolphins and most other members of *Cetacea*. The low frequency region includes frequencies below 200 Hz (generally restricted to the large whales). The high frequency region includes the frequencies associated with the larynx, from 200 Hz to 30 KHz. The ultra high frequency region is associated with the nasal features between the larynx and the blowhole and extends from 30 kHz to higher values.

### 1.1.2.1 Modification of the non-neural auditory system

The changes in the non-neural portions of the auditory system have been so large as to escape clear documentation until at least 1993[43]. Ketten has provided a major discussion of the morphology of the ears of Cetacea but it does not address the physiology as specifically[44]. It is now generally recognized that the exterior ear (the pinna) and the auditory canal of the mammalian template are highly atrophied and not used in *Odontocetea*. The remaining bridge between the hearing system of the typical terrestrial mammal and the cetaceans are the sea lions (Classification: Suborder Pinnipedia, Family Otariidae, Subfamily Otariinae, Genus Zalophus, Species californianus). They are one of the few members of their Suborder with conventional external ears and they use them when on land in the conventional manner, for communications.

As late as 2001, Supin, Popov & Mass were still unable to express how odontocetes acquired the acoustic energy used in hearing[45]. They assert without conviction, "All hypotheses of functioning of the ear in cetaceans imply delivering the sound to the middle ear." and "it remains debatable how sounds are delivered to the middle ear." As will be shown below, both the "auditory canal and the middle ear are non-functional in odontocete hearing.

#### 1.1.2.1.1 Introduction to the outer ear of the dolphin

The most detailed data on the outer ears of the dolphin appear to be that of Ketten. She has focused her early career on the anatomy and morphology of *Cetacea*, and primarily dolphins. She notes early in her writing of 2000 that the conventional pinna and auditory canal are not functional in cetacean hearing. "In general, odontocete external canals are plugged with cellular debris and dense cerumen, becoming progressively narrower, and ending in a blind caecum that has no observable connection

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[42]Porter, M. Siderius, M. & Kuperman, W. *ed*. (2004) High Frequency Ocean Acoustics. NY: American Institute of Physics Preface

[43]Au, W. (1993) The Sonar of Dolphins. NY: Springer-Verlag pp 26-30

[44]Ketten, D. (2000) Cetacean ears In Au, W. Popper, A. & Fay, R. *eds*. Hearing by Whales and Dolphins. NY: Springer Chapter 2

[45]Supin, A. Popov, V. & Mass, A. (2001) The Sensory Physiology of Aquatic Mammals. Boston, MA: Kluwer Academic Publishers pg 181

with the tympanic membrane or temporal bones."

The function of the conventional outer ear is provided by an alternate external ear structure based on an acoustic lens concept rather than an acoustic horn. The acoustic lens is well-understood technology in engineering. It is the specific configuration and density of all of the relevant structures along the inner jaw of the dolphin that remains poorly understood. This problem is complicated by the apparent ability of the dolphins to change the exterior contour, and probably the interior geometry of their outer ears. Field studies have shown the two outer ears achieve a very broad acceptance angle in the high frequency regime below 30 kHz but achieve a significantly narrower forward projecting beam angle in the 120-150 kHz range.

> Although suggested frequently by those unfamiliar with antenna theory, the lower jaw of the dolphin is not well configured to form a receiver of acoustic energy in the dolphin. Considering the jaw alone (or any fatty mass within the bone), its geometry and material properties are not well matched to the requirements for a high gain, narrow forward receiving angle, end-fire antenna (receiver). Alternatively, it has been suggested that the teeth might form an acoustic antenna array providing a high gain, narrow angle, end fire receiver. However, the teeth of the dolphin are not spaced appropriately to provide an efficient antenna at the frequencies employed in echolocation.

As Ketten notes, ". . . the bulk of recent experimental and anatomical studies indicate specialized fatty tissues in the jaw region are the primary route for conveying sound to *odontocete* middle and inner ears." Her 1998 work has provided additional details related to the arrangement of the fatty channels along the inner jaw[46]. **Figure 1.1.2-2** reproduced from that work shows the level of detail available concerning the fatty channel material in bottlenose dolphins. It does not appear the fat deposits operate in the mode suggested by her caricature. Her caricature appears to interpret the data collected by Brill[47] (and by others) using an overly restrictive neoprene hood. This hood prevented sound from reaching the outer sides of the jaw as well as the more important fatty tissue to the rear of the jaw on each side (the actual location of the outer ear). A less restrictive hood would have demonstrated that the fatty tissue along the sides of the rostrum played no role in hearing. This fact is demonstrated more uniquely by the receptive field pattern of the ears which is precisely that expected of a horn aperture of the size found in adult dolphins (**Section 1.1.3.1**).

Further definition of these fat deposits will be found below. [xxx need to define Is. ]

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[46]Ketten, D. (1998) Dolphin and bat sonar: convergence, divergence, or parallelism *Fourth Internat Biosonar Conf* pp 1-43

[47]Brill, R. (1986) The jaw-hearing dolphin: preliminary behavioral and acoustical evidence *In* Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pp 281-287

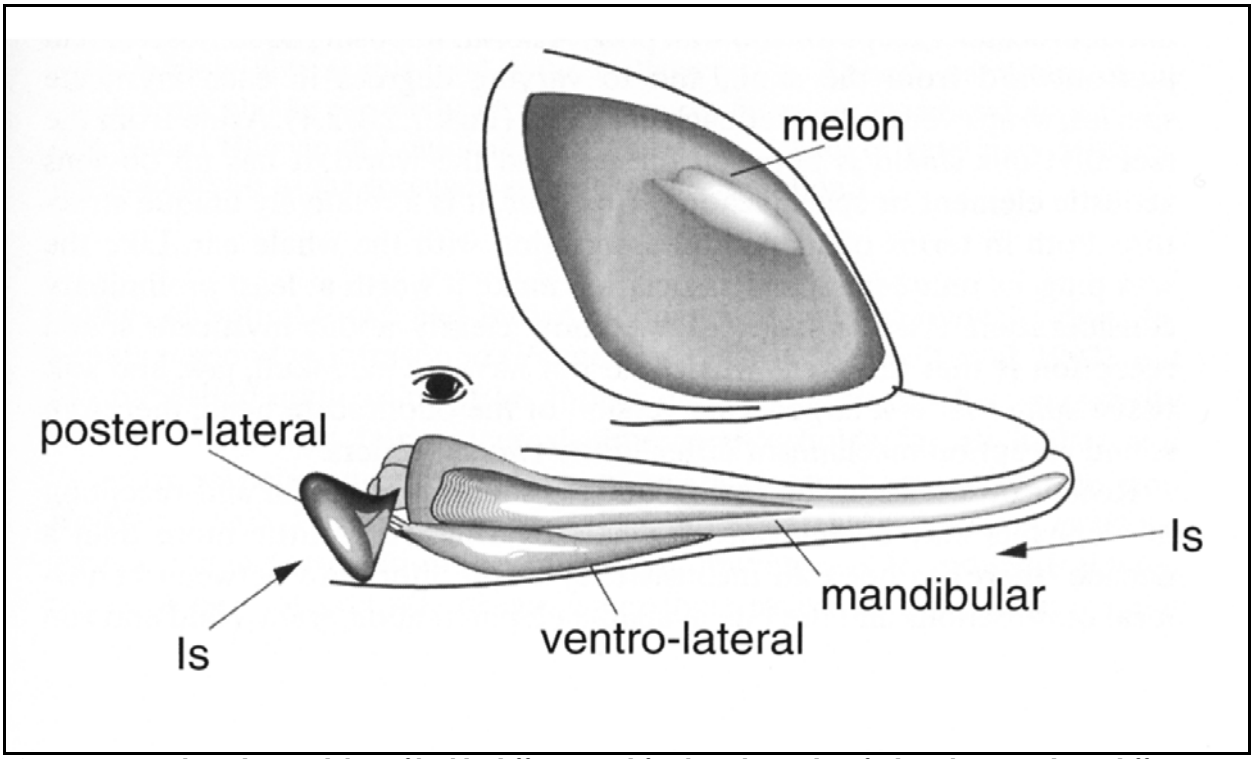


**Figure 1.1.2-2** Three discrete lobes of highly differentiated fats have been identified, each oriented in a different axis, which may act in a tripartite sound collecting array in odontocetes. From Ketten, 1994 & 1998.

### 1.1.2.1.2 Introduction to the outer-to-middle (or inner) ear interface in the dolphin

Au, writing in 2000, relied upon a caricature from McCormick (1970) to illustrate the middle ear of the bottlenose dolphin. The sketch and discussion are not definitive as to how the sound from the outer ear is transferred to the inner ear. He notes when discussing *T. truncatus*, "There is no direct connection between the tympanic membrane and the malleas." It is surmised that the acoustic energy within the mandibular fat channel are delivered to the vestibule of the inner ear via a thin walled portion of the vestibule itself.

Ketten approached the question differently. "In modern Cetacea, the ear bone consists of two connected bullae, properly called the tympano-periotic complex, that differ from temporal bone complexes of other mammals in form, construction, position, and, possibly overall function." She notes, "There is considerable debate at the current time concerning the function of the middle ear space in cetacean hearing." As noted above, it has no function in the hearing of *Tursiops truncatus*.

If the energy was transferred to the malleus by one of the ligaments, an evolutionary variant of the system would be able to operate in two modes, as in the sea lion. In that variant, the acoustic energy from the auditory canal would be introduced by the malleus from the tympanic membrane. The acoustic energy from any aquatic source would be introduced by motion of the external wall of the bulla and the appropriate ligament.

Since no impedance matching is required between the mandibular fat channel and the fluids of the vestibule associated with the inner ear, the acoustic energy may be delivered directly to the

vestibular fluid where it can be applied to the cochlear partition of the inner ear. Under this assumption, all of the bones of the middle ear are archaic and unused in the dolphin. The energy is delivered directly to the large vestibule of the otherwise atrophied vestibular portion of the labyrinth system and then converted into a surface acoustic wave traveling along Hensen's stripe on the tectorial membrane as in other mammalian inner ears.

Another feature of the middle ear concerns the thick vascularized mucosa, the corpus cavernosum, that lines the chamber. It is highly distensible and capable of filling the chamber (Ketten, 2000). While it is known that air fills the chamber in animals at the surface, the character of the chamber during diving is not currently known.

Ketten notes, "The tympano-periotic complex resides outside the skull in an extensive peribullar cavity." Comments occur in the literature suggesting the movement of the internal ears nearer the periphery of the head in large animals would aid in the binaural location of passive sound sources and the reflections from illuminated targets. Such an assertion appears largely irrelevant since the relevant binaural distance is measured between the centers of the external ear collection areas and has little to do with the location of the internal ears. This feature would need to be examined in terms of the additional delay associated with the slow projection of neural signals from the internal ears to the brain stem.

### 1.1.2.1.3 Introduction to the inner ear in the dolphin

The inner ear of the dolphin is contained in a boney mass that is acoustically isolated from the rest of the bones of the head to the greatest degree possible, as developed below. The energy from the outer ear is applied to a thin wall of the vestibule distinctly separate from the oval window used by terrestrial chordates. Form there, the energy is translated into a slow acoustic traveling wave proceeding to the tectorial membrane just as in other chordate ears.

Except for the greater degree of rigidity built into it, the cochlea is a conventional mammalian cochlea in most respects. Au presented considerable data in 1993 based on the investigations of the Wever team in the 1970's. Its most important functional characteristic is the low rate of curvature of Hensen's stripe in the basal region. This feature provides the high frequency performance, and the good differential frequency performance in that region, of the dolphin cochlea. The number and arrangement of inner and outer hair cells are virtually identical to that in the human. Another significant feature is the very large number of ganglion cells emanating from the spiral ganglia and forming the auditory nerve. The ganglia are about three times more numerous than in the human.

When discussing the inner ear, Ketten noted the minuteness of the vestibular system, associated with the inner ear, in dolphins. It appears the circular canals are minimally functional in the dolphins. As a result, the animal probably has little sense of up or down except as determined from the surface reverberation signals obtained from the echolocation system.

A significant difference in the inner ear of Cetacea compared to other mammals involves the outer ear to inner ear interface. In Cetacea, the energy from the outer ear is applied to a different wall of the vestibule than in other mammals. Terrestrial mammals introduce sound energy into the vestibule through the oval window (and the associated stapes). In Cetacea, the stapes and oval window have atrophied. The sound energy is introduced into the vestibule through the operculum, an acoustically pliable wall of the vestibule chamber as shown in **Figure 1.1.2-3**. The distance between the ears of the bottlenose dolphin is approximately the same as in humans, $Y_O \simeq 8$ inches. However, the effective aperture of each external ear is much larger, $X_O \simeq 3$ inches.

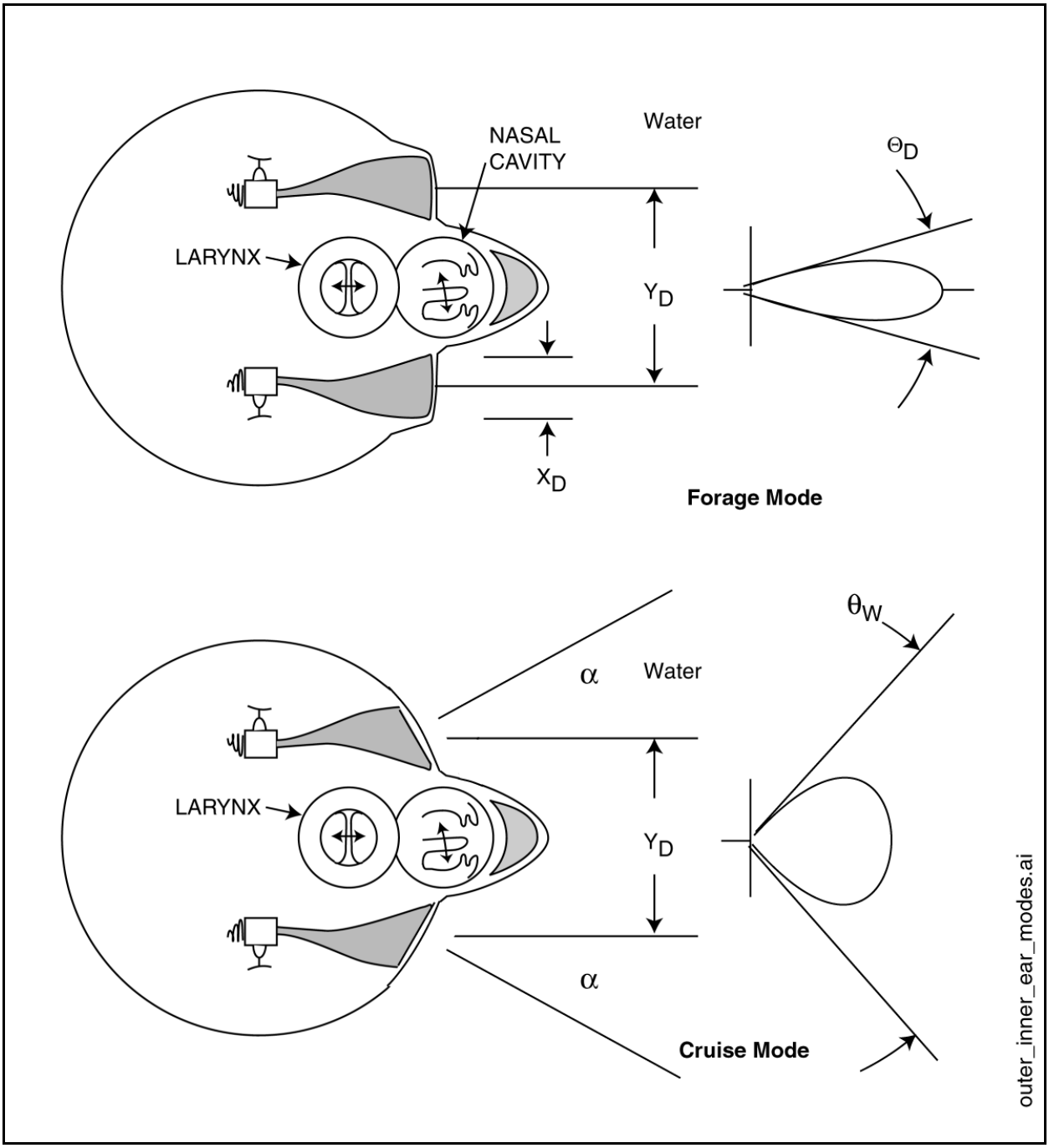


**Figure 1.1.2-3** The anatomy of the outer/inner ear interface of the dolphin. Note the atrophy of the meatus/stapes/oval window. Sound enters the vestibule of the labyrinth from the Luneberg (non-imaging) lenses forming the external ears of dolphin (shown shaded) through the operculum (a different wall) of the vestibule and proceeds to the cochlea. Top; the configuration of the areas adjacent to the lower jaws during foraging. Bottom; the configuration of the areas adjacent to the lower jaws during cruising (at speed). The field patterns on the right show the nominal situation from vectorially summing the field patterns of each ear. The angle $\theta_W$ significantly exceeds the angle $\theta_D$.

As will be discussed below, the calculated far-field acoustic pattern of each ear, acting as an acoustic antenna during foraging, is in excellent agreement with measured values of Au and colleagues. The required information concerning the dimensions of the outer ear aperture and the manipulation of the energy received at the aperture during cruise mode (the dolphin streamlined for operating at speed) are currently unknown. However, from basic principles of antenna theory it is reasonable to predict a much broader field pattern for the auditory system in cruise mode.

Thewissen has provided an actual picture of the bulla ear of the current dolphin[48], **Figure 1.1.2-4**, along with a picture of a predecessor of the dolphin known as Pakicetus. The bulla (also called the tympanic bone) constitutes the outer shell of both the middle and inner ears. It exhibits a very thick outer wall, the involucrum, and the very thin inner wall, he names the tympanic plate. Thewissen asserts the acoustic energy from the outer ear passes through the tympanic plate. Quoting Thewissen, "All cetacenans have a tympanic bone, with a tympanic plate and an involucrum, and no other animal is known to have one." "So for an anatomist, the ear makes the whale." Thewissen notes the atrophied condition of the small middle ear bones (the ossicles) in both specimens and that the incus (anvil) recovered from the archeological specimen was the size of a grain of rice compared to the tympanic bone shown being the size of half of a walnut. No recognizable oval window is present in the bulla of the modern or ancient dolphin. The thin wall of the tympanic plate is consistent with the above diagram with the thick wall of the operculum providing the necessary rigidity and structural strength.

[48]Thewissen, J. (2014) The Walking Whales: from land to water in eight million years. Oakland, Calif: Univ of California Press

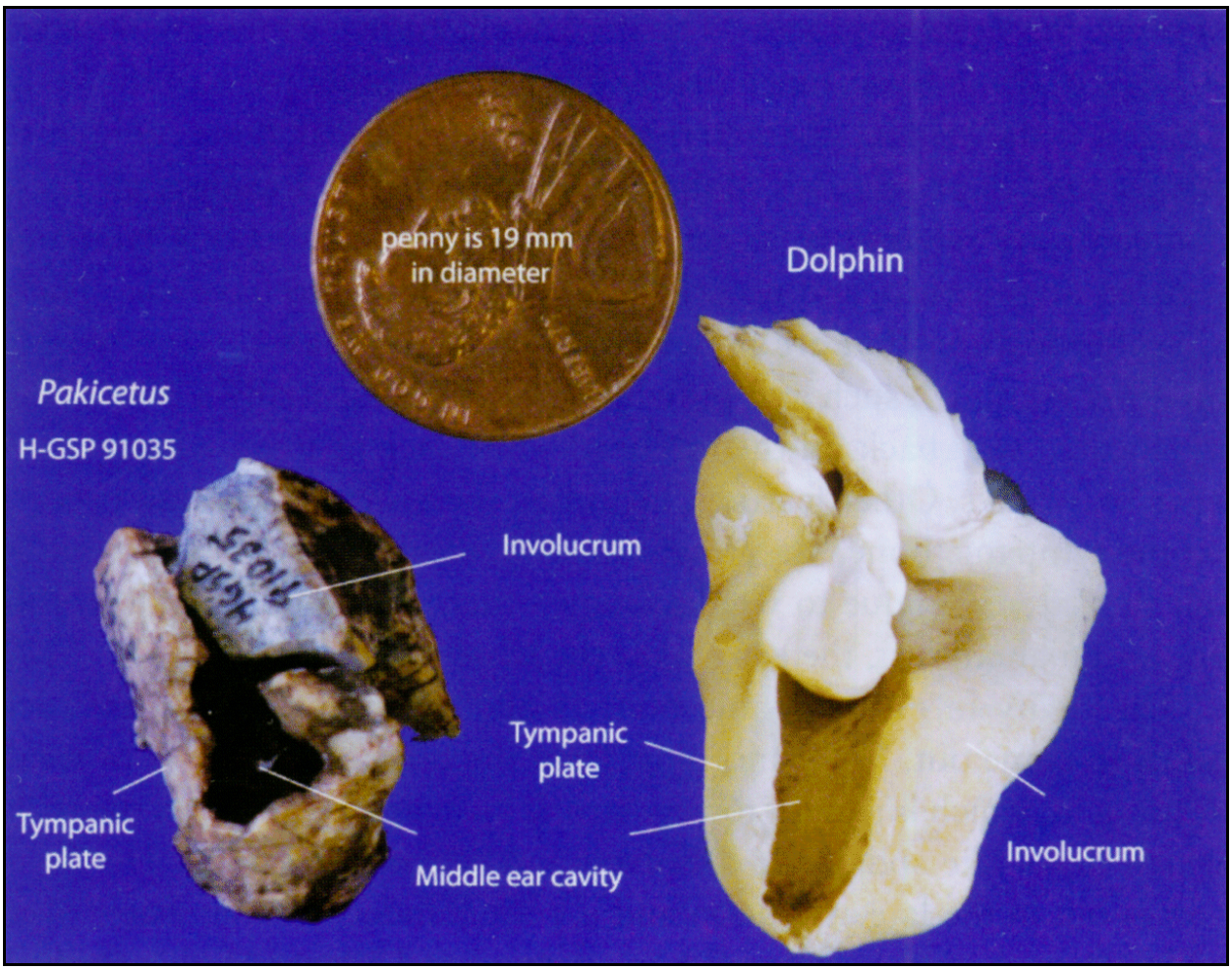


**Figure 1.1.2-4** The inner ear of a modern dolphin and a predecessor, Pakicetus fo 50 million years ago. The complete outer bone is called the bulla. It exhibits a very thin tympanic plate and the much thicker opposite involucrum. The minor bones of the middle ear have atrophied in both cases. See text. From Thewissen, 2014.

**Figure 1.1.2-5** shows a proposed configuration of the middle/inner ear of the dolphin based on an evolution from the equivalent structures in a terrestrial mammal. Thewissen has introduced labels for individual portions of the bulla (tympanic bone). Which of the labeled walls of the proposed configuration corresponds to his labels is currently unknown. It is rational to think of wall #2 as his involucrum because the semicircular canals of the terrestrial mammal are underdeveloped or absent in the dolphin. As a result, the wall #2 may be thicker than necessary.

The key point is that the entrance to the middle ear cavity provides more than adequate space for a fatty pad to extend from the skin of the dolphin to the wall of the vestibule without passing through any boney structure. The formation of an alternate window in the wall of the vestibule should not be difficult since the feature is initially formed of cartilage that may have remained non-calcified.

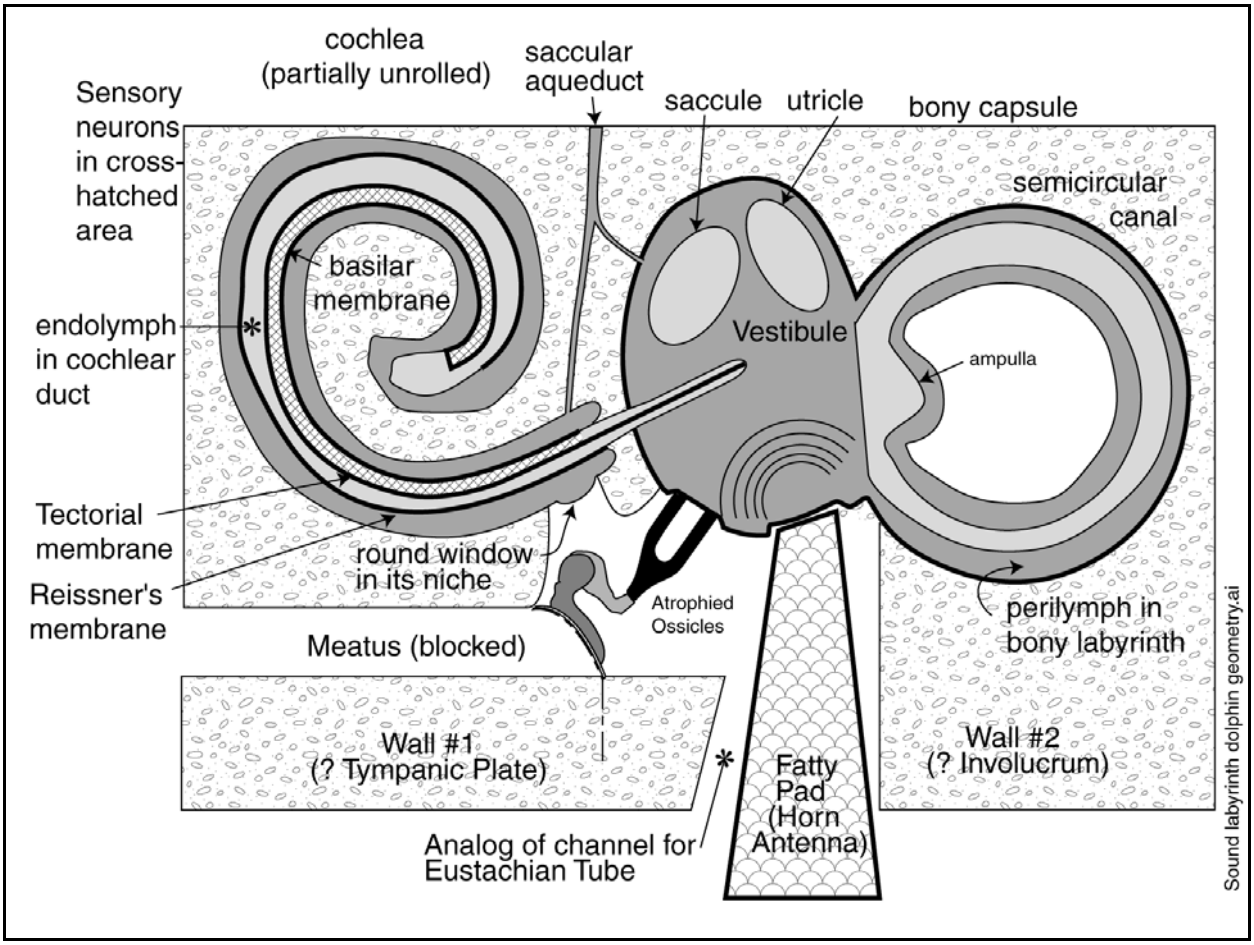


**Figure 1.1.2-5** A potential histological outer/inner ear interface for the dolphin. The middle ear is shown as totally atrophied and the meatus blocked. Acoustic energy is applied to the caecum of the inner ear within the vestibule through an alternate window formed by non-calcified cartilage. The semicircular canals are underdeveloped or non-functional in the dolphin, suggesting wall #2 might have absorbed the real estate associated with the canals and become thicker than necessary.

### 1.1.2.2 The expansion of the auditory neural system

**Figure 1.1.2-6** illustrates the major changes to the neural system schematically as they apply to the auditory system. The major changes involve the outer ear (which has changed beyond recognition from a morphological perspective), the major expansion of the lemniscus area and the geniculate nuclei (relative to their size in humans), and the close integration of the vocal and auditory systems in order to achieve their synchronous operation.

It should be noted that the vestibular system is proportionately much smaller in dolphins than in humans and other mammals of similar size. Its nearly vestigial size suggests that orientation with respect to the gravity vector is much less important in the dolphin than its orientation with respect to its acoustic environment. This leaves the arrangement of the chambers immediately behind the stapes and oval window unclear. It will be assumed the common chamber, known as the vestibule and normally found behind the oval window, is still there and it supports the transfer of longitudinal

acoustic waves within the vestibule to surface acoustic waves on the surface of the tectorial membrane (Fulton, 2006). Nachtigall (p. 96) has discussed the transfer of acoustic signals from the fatty channel of the outer ear directly into the vestibule without reliance upon the ossicle bones of the middle ear. Johnson has also discussed schematically the transfer of energy to the fluids of the inner ear by bone conduction[49].

[49]Johnson, C. (1986) Dolphin audition and echolocation capacities *In* Schusterman, R. Thomas, J. & Wood F. *eds*. Dolphin cognition and behavior: a comparative approach. Hillsdale, NJ: Erlbaum Assoc pp 115-136 Chapter 5

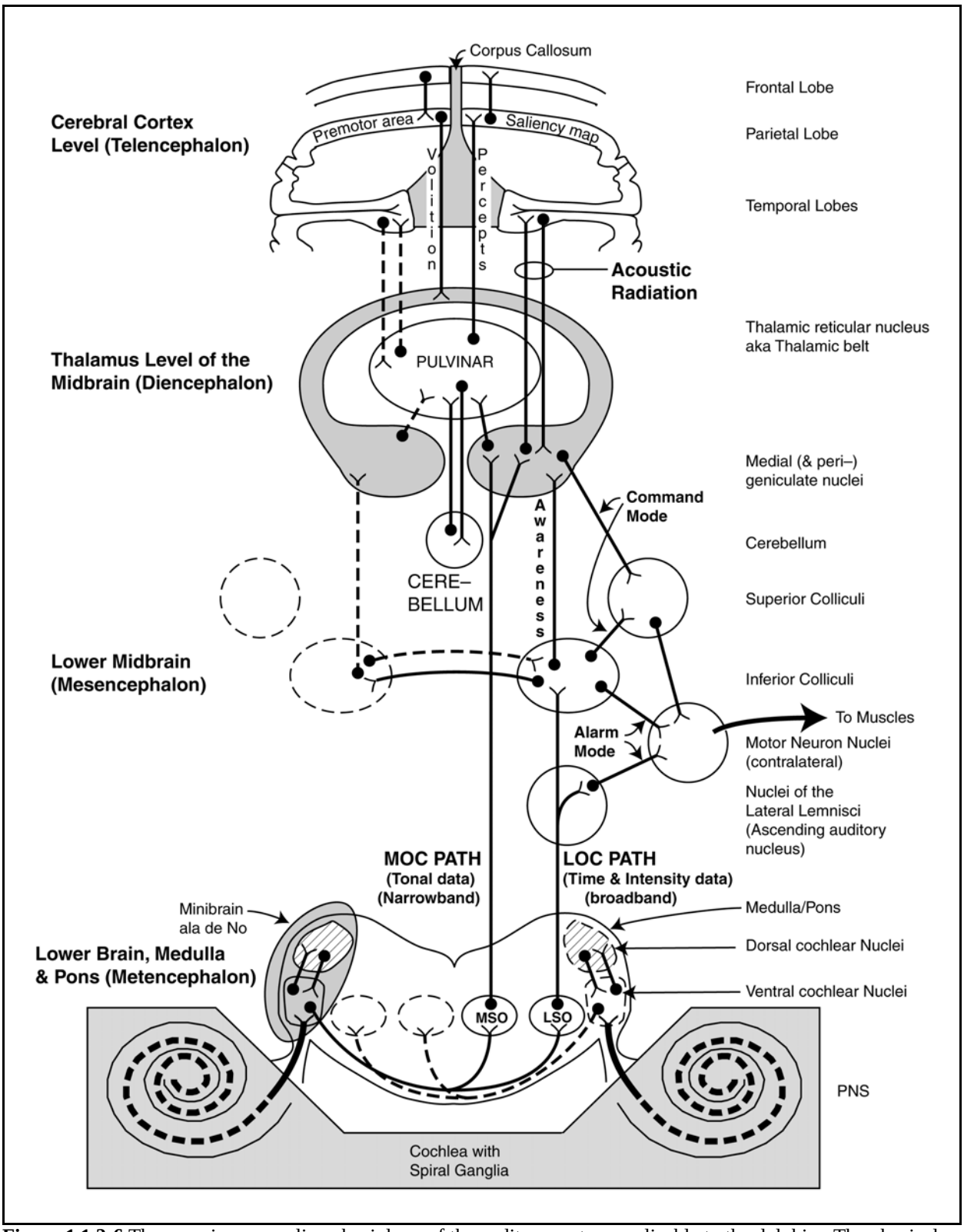


**Figure 1.1.2-6** The generic mammalian physiology of the auditory system applicable to the dolphin. The physical proportions of these elements differ greatly from their counterparts in humans. The lateral lemniscus is almost vestigial in humans but massive in the dolphin. From Fulton, 2006.

### 1.1.2.3 The expansion and optimization of the phonation system

As Cranford noted (p. 144), the production of simultaneous whistles and clicks from the dolphins have been reported many times over the years. However, only in the last five to ten years has it become clear how this is accomplished. The structure of the larynx and nasal passages of the bottlenose dolphin differ significantly from other species.

#### 1.1.2.3.1 The composition of the melon in the dolphin

Morris (p. 370-377) has discussed the evolution of the head and jaw fats in *odontocetes*. The variation in the density of these fats and their approximate changes in formula are well documented at a coarse spatial level. However, the data is too coarse to define the beam forming capabilities of the melon in signal generation and the material along the lower jaw of these animals in signal reception.

#### 1.1.2.3.2 The efficient generation of sound by *Cetacea*

Rodionov & Markov have addressed the production of sound within the nasal passages and indicate the subject is still very much open, including a change in perspective from their earlier writing[50].

Aroyan, et. al. have addressed the constraints on the generation of sound within Cetacea[51]. Both the high frequency regime of the bottlenose dolphin and the low frequency regime of the blue whale were addressed. The necessity of generating the low frequency acoustic signals within an air-filled cavity are stressed. The overall presentation stresses the very limited knowledge available at that time concerning sound generation in these animals.

Not addressed in the current literature are the optimal methods of generating the various frequencies used in dolphin echolocation. A conventional larynx is only capable of generating fundamental frequencies up to about 1000 Hz. Above that level, the aural cavity is used to select the higher harmonics of the fundamental when desired. To achieve fundamental acoustic frequencies above 5000 Hz using a stretched membrane is difficult because of the fragility of the resulting membrane (note the frequently broken strings on a violin). At the high frequencies used for echolocation, a different method of sound generation is desirable (required).

The efficient generation of high power density single cycle pulses by Cetacea is not well understood at present. The conventional wisdom is largely conceptual. It has been that air is moved passed a set of phonic lips to generate such a signal. The material characteristics of these lips has not been described in detail. However, it is not likely they are calcified like teeth.

In an alternate mechanism, the dolphin could achieve high power efficiency in its highest frequency sound generators by using an impact to excite a liquid crystalline fluid contained within the bursae of the phonic lips. Because of their low propagation velocities, liquid crystalline materials are able to generate quite high frequency oscillations within physically small spaces. The oscillatory energy originates in the material of the bursae rather than in the pneumatic spaces.

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[50]Rodionov, V. & Markov, V. (1992) Functional anatomy of the nasal system in the bottlenose dolphin *In* Thomas, J. Kastelein, R. & Supin, A. *eds*. Marine Mammal Sensory Systems. NY: Plenum pp 147-177

[51]Aroyan, J. McDonald, M. Webb, S. et al. (2000) Acoustic models of sound production and propagation *In* Au, W. Popper, A. & Fay, R. *eds*. Hearing by Whales and Dolphins. NY: Springer Chapter 10

The liquid crystalline material will conform to the dimensions of its container. This allows the fundamental frequency of the oscillations to be varied by changing the dimensions of the bursae under muscular control.

The oscillations within the bursae can be transferred to the melon by employing intermediate materials with a gradation in propagation velocities until a velocity approximating that found in sea water is reached. Such gradations have been recorded in the melon as noted above.

### 1.1.2.3.3 Alternate methods of high frequency sound generation

[xxx edit ]
There are several methods of sound generation that do not involve the flow of air past a pair of lips or the slamming together of two hard surfaces. One involves a temporary reduction in pressure in a relatively large volume and its rapid recovery, typically described as an alveolar click. A second involves a similar but more severe reduction in pressure resulting in a vacuum bubble in a gas or a vapor bubble in a liquid that can collapse upon a return of higher surrounding pressure. This action is related to cavitation.

A velaric sound results from the movements of the tongue. It is produced by the release of a closure at the front part of the tongue while the back of the tongue forms a second closure. The blade, tip or side of the tongue move down, releasing the front closure so that air rushes into the mouth, equalizing air pressure (ibid.: 247). The sounds produced by velaric airstream are called clicks.

A more promising mechanism for high power, high frequency sound generation is similar to the action of the tongue and front pallette in humans when making a clicking sound. Rather than slamming two surfaces together, the tongue is separated from the pallette quickly, resulting in a brief cavitation in the air within the oral cavity. If the tongue could move at a few hundred cycles per second (well within the range of human vocal chords), it could generate a series of clicks very similar to those of the dolphin. Under this scenario, the phonic lips are actually a phonic tongue and pallette. Cavitation can generate very significant acoustic forces. Cavitation is known to cause the pitting of ship propellers. In this case the energy would be transferred to the bursae forming the functional equivalent of a pallette. The biological nature of the tissue involved would allow the repair of any damage due to cavitation over time.

The oscillations within the bursae can be transferred to the melon by employing intermediate materials with a gradation in propagation velocities until a velocity approximating that found in sea water is reached. Such gradations have been recorded in the melon as noted above.

### 1.1.2.3.4 The generation of the high frequency sound fields

Rommel (Reynolds et al, p. 55) provided an early caricature of the fundamental modifications to the throat of the dolphin. Although not of current interest, it did discuss several important features of the system. It is the oldest figure found that describes the complete isolation of the tracheal path from the esophageal path. As a result, there is no need for an epiglottis. This separation allows the independent operation of these two systems.

Ridgway has confirmed to this author (personal communication) that sound generated by the bottlenose emanates exclusively from its blowhole. Questions remain as to the precise source of the different sounds generated by the bottlenose. Wesley (personal communication) has suggested to this author that the larynx has become extraneous to both the whistle and click generation process. He believes the phonic lips are responsible for both of these classifications of sound.

### 1.1.2.3.5 The potential generation of dual click sound fields

Johnson discusses an important point[52]. "Evans[53] showed that the beam pattern for different pulses can vary greatly, and that *T. truncatus* can emit two simultaneously, one 20° to left of center and one 20° to the right, separated in time by about 80 microseconds, with both appearing together at 0°" If confirmed, this observation justifies a significantly different interpretation of the sound generation facility of the bottlenose dolphin.

Bullock & Gurevich (p. 87) quote Reznikov as claiming the far field pattern of the high frequency click is rotated at high speed independently of any head motion[54]. The instrumentation to achieve the Evans and the Reznikov measurements with precision is not trivial.

Ridgway & Carder have noted two separate nasal passages begin immediately below the blowhole in the white whale, *Delphinapterus leucas*[55]. They have also noted that if an open catheter is placed in the blowhole, the animal is unable to generate significant sound intensity levels. This fact seems to confirm the pneumatic resonance form of sound generation as opposed to a potential mechanical resonance phenomenon.

Cranford has determined the shape of the melon in the spinner dolphin in considerable detail[56]. As in most dolphins, the melon is not symmetrical where it interfaces with the nasal passages. Cranford estimates the left branch (with its bursae) of the melon is rotated 50° down relative to the mid sagittal plane.

The recent detailed imaging of the pneumatic system in bottlenose dolphins in-vivo by Cranford, Amundin & Norris has confirmed only one larynx but dual pneumatic passages beyond the larynx until near the blowhole[57]. At the 2000 Acoustical Society Convention, the Cranford team asserted their records confirm independent and/or simultaneous pulse operation of the sets of phonic lips. They also assert they observed whistles from only the left phonic lips.

### 1.1.2.3.6 An alternate schematic for the generation of the high frequency sound fields

The work of the above investigators leads to a different schematic of the sound generation system in dolphins from that proposed earlier by Rommel. **Figure 1.1.2-7** illustrates the current

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[52]Johnson, C. (1986) Op. Cit. pg 126

[53]Evans, W. (1973) Echolocation by marine delphinids and one species of freshwater dolphin *J Acoust Soc Am* vol 54, pp 191-199

[54]Bullock, T. & Gurevich, V. (1979) Soviet literature on the nervous system and psychobiology of cetacea *Internat Rev Neurobiol* vol 21, pp 47-127

[55]Ridgway, S. & Carder, D. (1986) Nasal pressure and sound production in an echolocating white whale, *Delphinapterus leucas In* Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pp 53-60

[56]Cranford, T. (1986) The anatomy of acoustic structures in the spinner dolphin forehead as shown by X-ray computed tomography and computer graphics *In* Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pp 67-77

[57]Cranford, T. (1996) Functional morphology and homology in the odontocete nasal complex: implications for sound generation *J Morphol* vol 228, pp 223-285

understanding of the morphology of the dolphin pneumatic system. Not shown are the additional multitude of air sacs surrounding portions of the melon and behind and below the spiracular cavities. These sacs provide effective acoustic mirrors that protect the brain case and the bulla containing the cochlea from the high energy acoustic energy delivered to the melon. They may also act to form the acoustic output beam in conjunction with the melon.

The dual channel character of the system is quite different from the preliminary description of the dolphin forehead presented in several forums by Aroyan[58]. His draft 2002 paper contains a mixture of morphology and soundings of the bottlenose dolphin, and caricatures of sound generation for a member of the super family *Delphinoidea* that is not homologous with the bottlenose. It also differs from the concept employed here in suggesting the UHF source employs;
1. A source mechanism of broadband pulses,
2. A damped resonator, and
3. A projector of the signal produced by the first two components.

In this work, it is suggested that the UHF system in T. truncatus consists of;
1. Two high frequency resonators acting as sources,
2. Two independently controlled envelope modulators of the Gabor type, and
3. A projector of the signals produced by the above first two components.

In the proposed configuration, the spectral width of the pulses would be less than one-third of the center frequency and would not normally be considered broadband by a communications engineer.

[58]Aroyan, J. (2002) Simplified models of the dolphin echolocation emission system
http://members.cruzio.com/~jaroyan/publications.html &
http://www2.cruzio.com/~jaroyan/Dolphin%20Model%204.htm

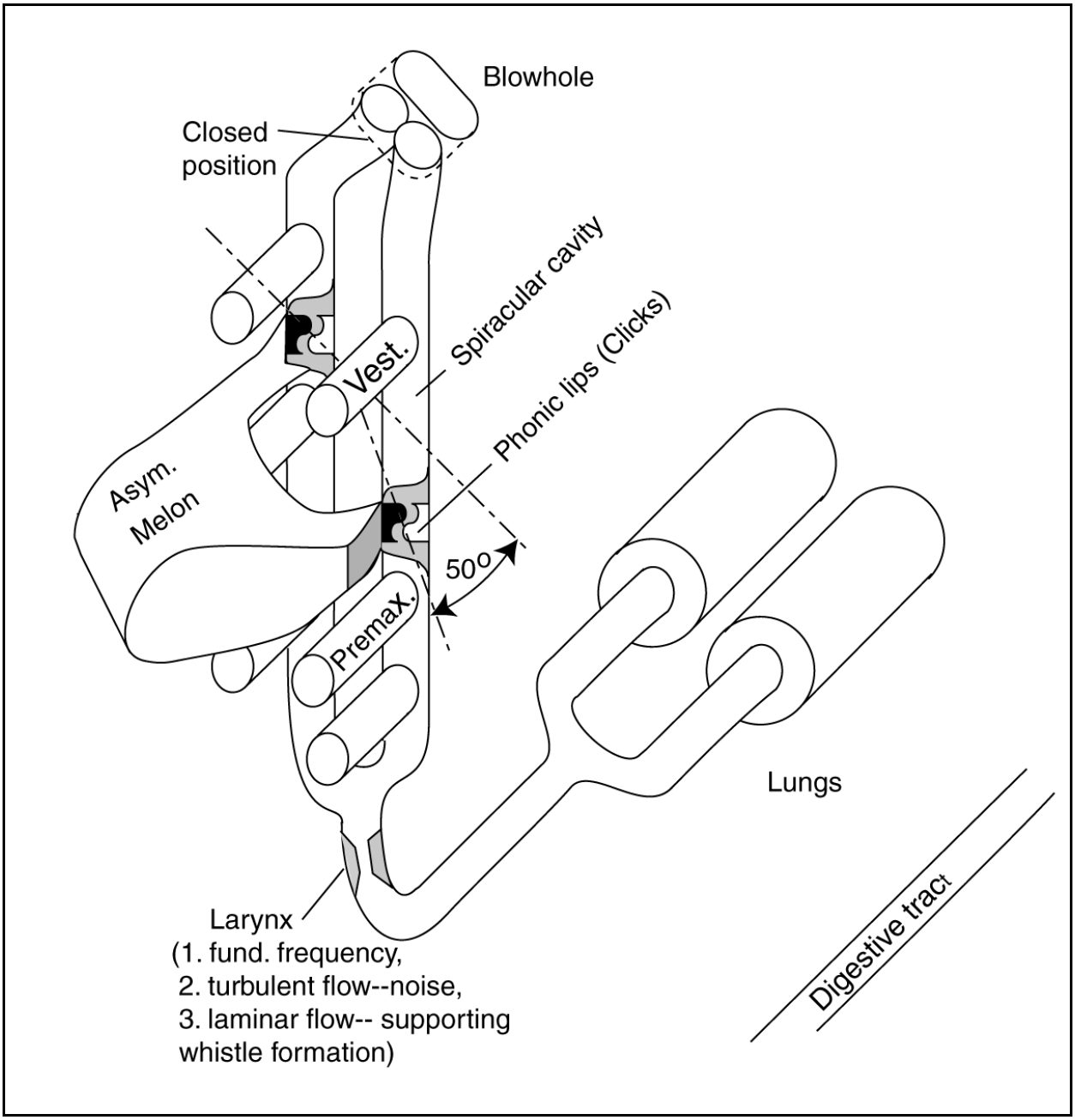


**Figure 1.1.2-7** The dual channel operation of the sound generation system in the bottlenose dolphin. This simplified schematic provides an explanation of several observed properties of the dolphins sound generation system. First, it isolates the sound generation system completely from the digestive tract. It provides two distinct air columns between the larynx and the blowhole. The individual sets of phonic lips can excite the melon separately and generate far field patterns that are significantly different (either simultaneously or sequentially. Note the angle between the plane containing the pairs of phonic lips and the horizontal plane.

The schematic is somewhat simplified in that Morris and others describe the movement of air from the premaxillary air sac upward past the phonic lips (more properly the valvular flaps of the nasal plugs according to Morris) into an accessory sac and finally into the vestibular sac. Whether the accessory sac is independent of the connecting spiracular cavity is difficult to discern from the

published record. Based on the work reported in **Appendix U**, there also may be multiple vestibular sacks separated by muscular channel walls that aid the generation of multiple formants simultaneously. It also appears the blowhole cover may be very effective in isolating the two channels, thereby allowing them to operate independently during vocalization.

While the generation of whistles and other sounds is associated with the larynx in this figure, some investigators believe the generation of whistles has migrated *exclusively* to the phonic lips or the channel segments operating as individual resonators. Additional data derived from sophisticated instrumentation (beyond the current behavioral evidence) will be required to confirm this point.

As noted in Appendix U, the larynx may operate in three distinct modes.

1. The laryngeal lips taut as the air is forced between them causing a fundamental frequency vibration rich in harmonic content.
2. The laryngeal lips formed so as to cause turbulent flow, thereby generating broadband noise absent any fundamental frequency component and supporting the generation of unvoiced sounds.
3. The laryngeal lips formed so as to allow laminar air flow, thereby supporting the generation of pure tones within the resonant sections of the individual channels of the nairs.

The arrangement of the elements in this schematic offers a much broader UHF (and possibly HF) capability than does a single channel system. These capabilities depend on the degree of separation of the two pneumatic channels and their arrangement immediately below the blowhole acting as a closure. If the blowhole caps the two pneumatic channels individually, they would continue to be describable as independent systems. However, if the blowhole only closes above a common space, then the overall system could also include a mode of operation where the pneumatic channels would be joined.

In either case, the parallel character of the phonic lips leads to a system capable of independent dual channel operation. This ability, at least in the generation of UHF clicks appears well documented and well supported by the detailed geometry of the melon. It leads to the generation of two independent forward projecting beams separated by a distinct angle as reported above. These beams may occur simultaneously or sequentially. Their generation is compatible with a distinct spatial polarization that may appear to be due to a rotating beam when measured with less than optimum instrumentation. The spatial polarization may lead to the reporting of a distinct temporal phase relationship between the two beams under these conditions.

By manipulating the volume of air in the air sacs and the volume of the lungs, the air captured within the animal can be circulated back and forth repeatedly as desired. Thus, the air in the left and right tracheal paths can be driven past a constricting larynx or the constricting nasal plug. The hatched area represents the boney character of much of the wall of the tracheal airway in dolphins. The nasal plug is shown as a specialized portion of the melon. This schematic would support the concept of dual sound sources within the trachea of dolphins. The larynx would produce sounds whistles within the frequency range and of the character normally associated with mammals of this size. The nasal plug would generate the higher frequency sounds associated with the precise echolocation facility of the dolphin. Mackay has confirmed the larynx is not the source of the high frequency sound energy based on magnetic resonance imaging in-vivo and during high frequency phonation[59].

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[59]Mackay, R. (1986) Whale heads, magnetic resonance images, ray diagrams and tiny bubbles In Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pg 82

Johnson has provided a schematic of the various air-filled spaces in the body of the dolphin[60]. The figure generally follows that shown here. It makes no reference to the vestigial meatus and pinna when discussing the dolphin auditory system.

Bullock & Gurevich (p. 74) provide a variety of details concerning the muscles and neurons associated with the air sacs, the spiracular cavity and the tissue near the blowhole. They also support the assertion by Marjov & Tarchevskaya (1978) that the dolphin can make a variety of sounds during exhalation and inhalation as well as during the apneustic plateau.

Cranford has performed an extensive investigation of the nasal spaces in *odontocetes* seeking the source of high frequency sounds[61]. However, the precise character of the blowhole closing could not be found in that study. Cranford does address the limited ability of the muscles (even selected muscles) to operate at rates above 800 actions per second. This led to a study of friction-based, cavitation-based and pneumatic mechanisms. His conclusion is that the source of high frequency vibrations is analogous to those generated in a brass wind instrument. He focuses on the importance of the vibrations existing in the structure of the phonic lips. This feature avoids the necessity of coupling the vibrations of the air column into the tissue of the animal before projection into the water environment. He supports his assertions with the results of the first reported set of high speed video endoscopy recordings. The high frequency clicks are formed by one cycle of the explosive parting and closing of the phonic lips. The waveform within the envelope of the explosion is apparently due to the mechanical properties of the lips (plug, etc.). His conclusion is that the dolphin can generate two independent acoustic signals using the two nasal passages (or potentially two locations along one passage). As others have noted, the sound generation complex on the right is approximately twice the size of that on the left in *T. truncatus*. Cranford also notes the potential difference in frequency between the simultaneous clicks from the same animal.

The generation of two distinct UHF beams of acoustic energy leads to the description of this part of the vocal system as bivocal or *biphonic* in analogy to the binaural operation of the two ears.

In this description, the temporal phase relationship between the two acoustic sources is an entirely different subject than the phase relationship between the signals generated within the outer and/or inner ears. The phase relationship between the two radiators could significantly affect the reflected signal from a target.

Cranford also noted another intriguing endoscopic observation in the dolphin. “the dynamic parallel furrows that form in the surface of the nasal mucosa, between the nasal plugs and the phonic lips. The direction and depth of the furrows can be changed instantaneously, apparently by muscle action.” This work suggests the mucosa is acting as a liquid crystal and the furrows are surface acoustic waves dependent on the size of the borders of the liquid crystal.

As a group, the above observations provide a strong foundation for the independent dual channel capability of the phonation system of the dolphin.

### 1.1.2.3.7 Acoustic propagation within the melon and other cavities of the dolphin head

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[60]Johnson, C. (1986) Dolphin audition and echolocation capacities *In* Schusterman, R. Thomas, J. & Wood F. *eds.* Dolphin cognition and behavior: a comparative approach. Hillsdale, NJ: Erlbaum Assoc pg 120

[61]Cranford, T. (2000) Op. Cit.

As noted by Cranford (p. 135), any study of signal generation would be incomplete without a consideration of the effect on signal propagation of the various regions of different density within the head of the dolphin. Not only are the densities of the various tissues and bones of the head significant, but the myriad air spaces represent near-perfect mirrors to the transmission of acoustic energy within the soft tissue of the head. He discusses these passages in reasonable detail but notes that their dynamic characteristics have prevented any definite conclusions to date (p. 123). Any significant ray tracing applicable to the head of the dolphin must take into consideration the instantaneous configuration of these air spaces. Cranford's concluding remarks (p. 141-145) concerning future directions for research are very useful to the research community.

### 1.1.2.3.8 Pulse repetition rates in high frequency echolocation

Odontocetes are known to vary the pulse repetition rate during echolocation so as to prevent multiple pulses to be propagating in the water simultaneously. At long range, the pulse rate is necessarily low. Pulses may be separated by 50 msec or more (20 pps). At close range, the pulses can be as close together as 1.5 msec (660 pps). Avoiding simultaneous pulses in the medium is of great advantage in simplifying the separation of multiple targets and the removal of signal clutter due to reverberation.

Cranford showed concern (p. 113) that subsequent pulses were frequently generated before the return signals were completely processed. In good radar and sonar system design, there is no need for the returning pulses to be processed prior to the generation of the next pulse. Once the returns have reached the neural system, they are isolated from the environment and can be processed "off-line" using a pipeline approach as long as the temporal integrity of the signals is maintained. Such a pipeline approach may even involve multiple parallel pipelines as long as temporal integrity is maintained.

It should be noted that 660 pps is near the limit of the firing rate of specialized neurons, such as those found in the precision optical system of mammalian vision, the binaural neural circuits of mammals, and probably in the precision echolocation system of the dolphin.

The unique characteristics of click trains in dolphins have spawned a number of specialized terms. The pulse rate of a rapid train of pulses can be heard by humans. This tone, defined by the pulse rate, has been labeled the "time-separation pitch." Cranford has noted the systematic variation in the number of pulses in a pulse train among different species of *odontocete*. He suggests those pulse trains of less than seven pulses be labeled oligocyclic. Longer trains would be described as *polycyclic*. It is too early to associate the other characteristics of a pulse train described by Cranford (p. 115) with these two labels unequivocally.

### 1.1.2.4 The unique neural circuits of echolocation

Several investigators have noted the unusually large size of some of the axons connecting the spiral ganglia to the CNS. Ridgway has considered the significance of these large axons primarily with respect to propagation delay times[62]. However, such axons are also capable of propagating wider bandwidth signals[63]. The size of these axons, and the identification of a unique operating regime

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[62]Ridgway, S. (1986) Physiological observations on dolphin brains *In* Schusterman, R. Thomas, J. & Wood F. *eds*. Dolphin cognition and behavior: a comparative approach. Hillsdale, NJ: Erlbaum Assoc pp 115-136 Chapter 2

[63]Fulton, J. (2006b) The Electrochemistry of the Neuron. Sec. 6.3.5 www.sightresearch.net/neuron/pdf/6Electrophysiol.pdf

extending from 0.2 to 0.9 kHz by Reynolds, suggest these axons are associated with phase-coherent processing of the signals delivered to the passive source location circuits, and probably the active echolocation circuits of the CNS. Data is beginning to accumulate suggesting the passive location circuits are located in the inferior colliculus and the active location circuits are located in the lateral lemniscus of the paleocortex.

Ridgway has noted that "Bullock & Ridgway suggested that the dolphin brain might possess two separate auditory systems, one specialized for ultra-brief, fast-rising sounds like echolocation clicks while th other was specialized for longer, slower rising sound like dolphin whistles."

### 1.1.3 Overview of signaling in dolphins

It appears generally accepted now that the dolphins make a variety of sounds for purposes of both communications and echolocation. The range of the sounds produced by *odontocetes* is so wide, they have been informally labeled "sea canaries." They may also generate high frequency signals for the purposes of stunning their prey. However, this latter subject is beyond the scope of this work. Bullock & Gurevich (and many others) have noted the wide variety of signals generated by dolphins. However, it has been difficult to categorize these sound in a non-overlapping matrix. Bullock & Gurevich described the possible sounds studied by Markov, et. al. and their permutations and combinations using thirty-one alphabetical symbols (fortunately Russian contains more letters than English) and five combinatorial rules. They did not attempt to associate semantic rules with these combinations. Others have described up to nine combinatorial rules. Caldwell et al.published large tables of the potential sounds from the bottlenose in captivity (which may not be complete because of this constraint)[64].

This work will only address the two major classes of dolphin sounds, clicks and whistles. Only those whistles having characteristics that might be associated with echolocation operations will be explored.

One of the obvious problems with studying the morphology of the dolphins is the apparent ability of the animals to dynamically change the physical shape of many of the elements employed in echolocation. The artistic and photographic figures in Reynolds suggest the wide variety of external head shapes encountered in dolphins under different conditions. As a result of this situation, most schematic drawings of the head of the dolphin in the technical literature must te taken as exemplary but not definitive of the class, or even the particular animal under different conditions.

Recent activity in dolphin research has been centered on understanding the detailed morphology of the echolocation apparatus in dolphins. Separate teams are exploring both the signal radiation and the signal reception systems. Aroyan has provided a useful pedagogical paper (in incomplete draft form) concerning the signal generation aspects for dolphins[65]. His modeling should not be taken as the precise model of the system but of a potential model. His reliance on a parabolic reflector based on the shape of the skull is probably over-constrained (particularly when compared to his figures 1 & 2). Alternate descriptions of the source that do not involve a broad band noise source are worthy of consideration. His figures 9 and 10 may only apply to a subset of *Cetacea* with only one functional

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[64]Caldwell, M. Caldwell, D. & Tyack, P. (1990) Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin In Leatherwood, S. & Reeves, R. *eds*. The Bottlenose Dolphin. NY: Academic Press Chap 10

[65]Aroyan, J. (2002) Simplified models of the dolphin echolocation emission system. http://www2.cruzio.com/~jaroyan/Dolphin%20Model%204.htm

source of high frequency pulses. There is considerable data supporting two active sources of high frequency pulses in *T. truncatus*. A point Aroyan does illustrate is the wide variety of waveforms generated by dolphins. It is not likely all of these signals can be generated by one geometrically fixed source. As in human speech, the variety of signal waveforms suggests a dynamic ability to vary the spatial geometry of both the source and beam forming elements of the system. Such dynamics makes precise description of the system difficult.

Potter & Taylor have provided an interesting Power Point presentation on a novel hypothesis that the individual teeth of the dolphin play a major role in the reception of acoustic energy[66,67]. Hoffmann-Kuhnt, Chitre & Potter have continued the study of this hypothesis and presented a paper discussing the application of sparse array signal reception applicable to the dolphin[68]. The paper makes a variety of assumptions concerning the nature of the receiver geometry but does not discuss the simple binaural character or the neural data processing associated with the hearing system. Their discussion of signal processing appears to relate more to their concepts of incoherent synthetic array signal processing than to the character of the receiving system in dolphins. This work will focus on simpler receiving configurations.

Houser, et. al. have continued a program of imaging the head of the dolphin using modern medical imaging techniques and included a thorough bibliography in their report[69]. An important observation was made in this paper. It is critically important that the cochlea of the dolphin be isolated from the high intensity (estimated 60 watt peak level) acoustic generator located less than twenty centimeters away. It is important that air sacs be provided to act as acoustic mirrors for two reasons. First, to aid in effective beam formation, and second, to shield the bulla containing the cochlea. Houser, et. al. noted, "Air spaces directly abutted the tympano-periotic complex such that a bone-air interface existed. Coverage was most complete on the dorsal medial and posterior surfaces of the tympano-periotic complex, with the dorsal surface being almost completely covered by a layer of air."

### 1.1.3.1 The external anatomy and beam forming capability of the outer ears

The outer ear of the dolphin has been so greatly modified that it is hardly recognizable within the framework of conventional morphology. Functionally, the morphological horn type energy collectors at each side of the head have been replaced by hydrodynamically-streamlined surface-mounted non-imaging lens-type energy collectors below each jaw. The conventional auditory canal (meatus) and pinna of the dolphin is considered vestigial and no longer associated with hearing.

For the remainder of this discussion, the "outer ear" of the dolphin will refer to these two fat-filled horn-type receiving devices at the root of the lower jaw and not the water-filled horn-type receivers left from the days the dolphin was a terrestrial animal. .

While many artistic and photographic renditions of the front quarter profile of the dolphin exist, it is

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[66]Potter, J. & Taylor, E. (2001) On novel reception models for bottlenose dolphin echolocation. www.arl.nus.edu.sg/objects/paper_ver1.pdf *Proc Inst Acoust* vol 23, pp 103-112

[67]Potter, J. & Taylor, E. (2002) On novel reception models for Bottlenose dolphin echolocation Http://www.arl.nus.edu.sg/objects/dolphin.ppt

[68]Hoffmann-Kuhnt, M. Chitre, M. & Potter, J. (Undated) "Ghosts in the Image: – aliasing problems with incoherent synthetic aperture using a sparse array. www.arl.nus.edu.sg/objects/0_327.pdf

[69]Houser, D. Finneran, J. et al. (2004) Structural and functional imaging of bottlenose dolphin (Tursiops truncatus) cranial anatomy *J Exp Biol* vol 207, pp 3657-3665

difficult to find one describing the outer ear appropriately. **Figure 1.1.3-1** shows a modified drawing, credited to Marya Willis-Glowka (Reynolds, p. 20), showing the location of the forward facing apertures of these fat-filled horns of the outer ear and the location of the vestigial auditory canal (now probably functioning as a static pressure port). The internal geometry of the "outer ear" forms a forward-looking beam at high frequencies but a more omnidirectional beam at low frequencies.

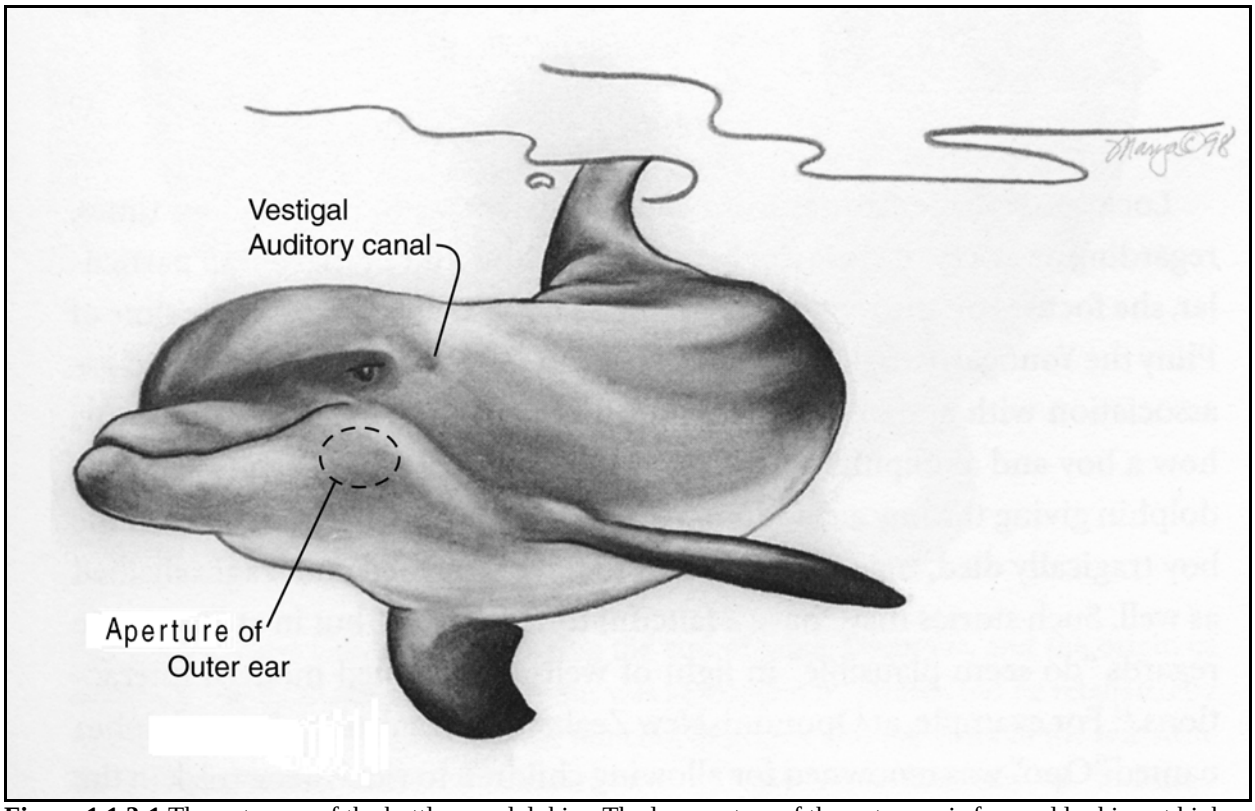


**Figure 1.1.3-1** The outer ear of the bottlenose dolphin. The lens system of the outer ear is forward looking at high auditory frequencies but nearly omnidirectional at low frequencies. The vestigial auditory canal (absent any pinna) may function as a static pressure port largely independent of the hearing system. Modified from Marya Willis-Glowka.

The forward-looking aspect of the hearing receivers (outer ears) is shown more clearly in **Figure 1.1.3-2**, modified from a photograph in Caldwell & Caldwell[70]. The variations in the prominence of the external ears in different renderings of the bottlenose dolphin suggest the shape of these features

[70]Caldwell, D. & Caldwell, M. (1972) The World of the Bottlenosed Dolphin. NY: J. B. Lippincott pg 108

may be changeable at will by the animal. Kassewitz has noted the great and rapid motility of the tissue in both the melon area and the lower jaw area of the dolphin (personal communication). This motility suggests the steerability of both the UHF sound generation system as well as the steerability of the reception system. The configuration of the radiating and reception elements of the echolocation system is similar to that described by Floyd in Nachtigall & Moore[71].

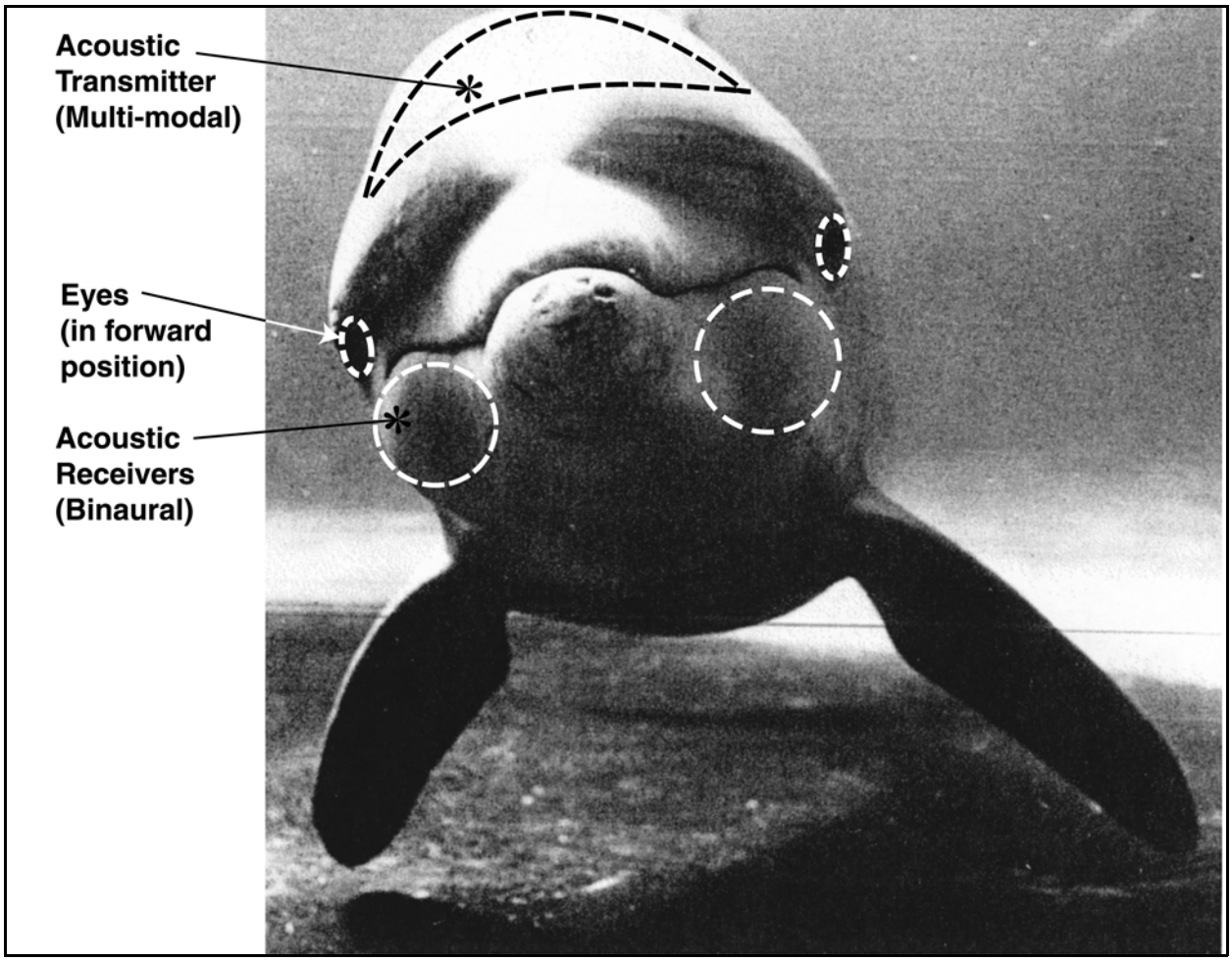


**Figure 1.1.3-2** A front view of the bottlenose dolphin showing the forward looking lens-type external ears and the general location of the melon used for echolocation (dotted overlays) . The caption of the Caldwell & Caldwell figure hint that the eyes and possibly the eye sockets of the dolphin may rotate to support their apparently good stereoscopic vision. The eyes are seen more clearly in the original art. Modified from Caldwell & Caldwell, 1972.

Before beginning to analyze the physiology of the echolocation system in dolphins, it is very important to note three unique conditions. First, the differences in acoustic impedance between air and both water and the soft tissue of the dolphin are so great that the air-tissue interfaces within the head of the dolphin act as acoustic mirrors[72]. Second, the wavelengths of the signals generated by

[71]Floyd, R. (1986) Biosonar signal processing applications *In* Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pg 779

[72]Ketten, D. (2000) Cetacean ears *In* Au, W. Popper, A. & Fay, R. *eds*. Op. Cit. pg 46

and received by the dolphin are frequently long relative to the dimensions of the animal and its relevant parts. Thus, the energy propagating internally and within about one-meter or less of the animal must be analyzed under near field conditions. This condition means that simple geometric ray tracing can only provide an approximation of what is actually occurring. A full diffraction-based ray tracing activity is required to obtain accurate results. Harris has reviewed the near field and far-field effects[73]. Mackay has also addressed the near field situation and suggested solutions using differential equations are required[74].

Third, investigators have frequently discussed the conduction of sound within the boney structure of the skull in mammals. In the dolphins, the auditory bulla has migrated to a point outside of the skull and it is not attached to the skull by bone. In addition, most of the potential sound conducting pathways with the dolphin are made of soft tissue. Therefore, the conventional physiological term bone conduction is probably best replaced by tissue conduction when speaking of dolphins, and probably other members of *Cetacea* (as suggested by Reppening in 1972). However, such a change in terms is unlikely in the short run.

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[73]Harris, G. (1964) Considerations on the physics of sound production by fishes *In* Tavolga, W. *ed*. Marine Bioacoustics. NY: Pergamon Press pp 233-247

[74]Mackay, R. (1986) Whale heads, magnetic resonance images, ray diagrams and tiny bubbles In Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pp 79-86

By employing gradient index materials in the fatty channel connecting these energy collectors to the bulla, excellent forward looking acoustic performance has been achieved at frequencies near 120 kHz. The field patterns become more omnidirectional as the frequency is reduced. The data is very sparse and generally obtained as a composite based on binaural hearing. Analyzing the data is awkward because of the limited data available on the geometry of the fatty channels behind the aperture. By decomposing the binaural field pattern, a first order estimate of the single-ear performance can be made. **Figure 1.1.3-3** shows how these patterns might look for the two ears individually. The asymmetry of the patterns would suggest the presence of an acoustic ground plane within the beam forming structure. This structure is probably the bone of the lower mandible. If the mandible is acting as a ground plane, it would explain the assertions that the mandible and teeth are areas of high auditory sensitivity in the dolphin when excited by a contact source of acoustic energy. Such excitation would not suggest the mandible is an active part of the beam forming elements of the receiver and would not be suggestive of the far field performance of the mandible.

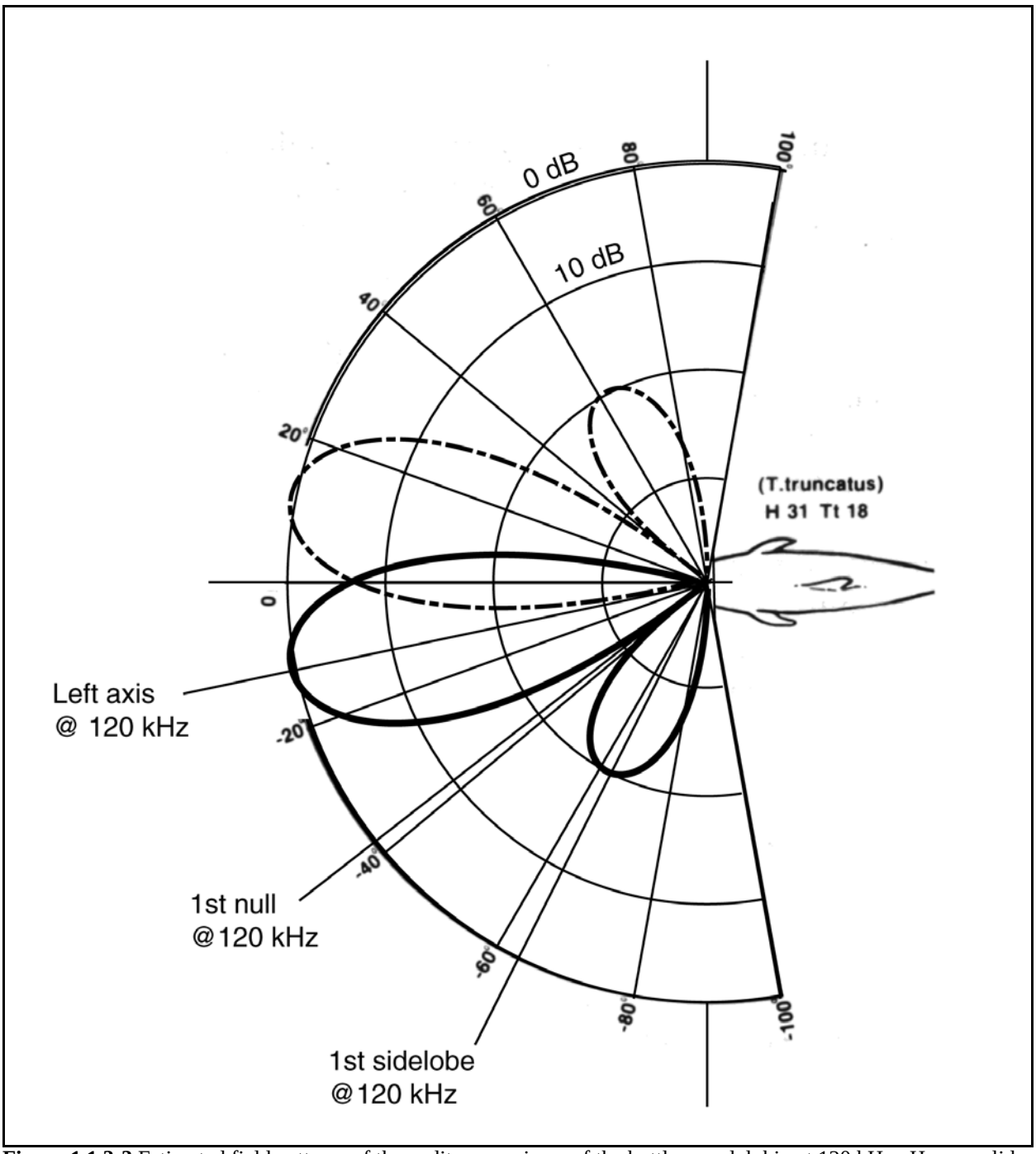


**Figure 1.1.3-3** Estimated field patterns of the auditory receivers of the bottlenose dolphin at 120 kHz. Heavy solid lines; left ear. Broken lines, right ear. The sum of these two patterns would result in a single pattern with a principle lobe along the centerline of the animal. From data of Au & Moore, 1984.

The overall field pattern due to one ear does suggest the fatty channel forms a conduit containing one or more reflective elements and/or refractive elements. The mandible would be an example of a reflective material. A variable index in the fatty channel itself would be an example of a refractive material. This fatty material is known to be heterogeneous (Morris, p. 369).

The small bones of the middle ear are not used in the hearing of Cetaceans. Ridgway notes the stiffness of the ossicles of the middle ear and the malleus does not attach directly to the tympanic membrane. The basilar membrane is within a mm or two of the length of the human membrane but it is more firmly supported at the basal terminus. The number of inner and outer hair cells appears to be comparable with the human but the number of ganglion cells in the spiral ganglia is much greater. Where the ratio of ganglion cells to hair cells is about 2:1 in humans, it is about 5:1 in the bottlenose dolphin.

The dolphin lacks a pinna and the external meatus has apparently become a vestige as will be discussed below.

Several current members of the dolphin family are described graphically by Au on page 136 and performance-wise on page 134. Chapter 2 describes the hearing system and Chapter 5 describes the active sound generation system. Chapter 10 describes the estimated signal processing capability of the species without the benefit of significant physiological data. The signal processing capability is derived primarily from performance data collected under a variety of conditions but without a good model of the biological systems involved.

The high frequency acoustic performance capability of the animal is very completely characterized in Au. However, the physiology of the individual acoustic elements within the head is not well detailed at this time. The discussions in Au of the beam forming capability of the dolphin and the signal processing capability (in analogy to other radars and sonars) are both elementary and should not be relied upon at the detail level. His section 10.3.5 agrees with this statement. Chapter 10 explored three signal processing models; an envelope detection model, a matched-filter model and a spectrogram correlation model. The comments concerning the time required to compute the spectrogram are largely irrelevant if the dolphin uses a spatial signal separator and spatial signal correlator as expected based on its generic mammalian hearing capabilities.

Au makes a number of important distinctions between the capabilities of bats and dolphins. He generally limits dolphins to short pulse (wide band) signal generation while bats are known to emit longer pulse (narrower band) signals when required to achieve a Doppler radar capability. While dolphins are known to use (and are trained to respond with) long duration whistles, it may be that these are generated by the larynx and not related to their sonar capabilities. On the other hand, it appears they are trained to whistle while underwater which suggests the inherent capability of achieving Doppler sonar performance using this lower frequency sound source (typically 5 to 30 kHz lasting up to several seconds; Au, page 77).

> The term broadband should be used sparingly when discussing the clicks of *odontocetes*. The envelope of the clicks in most species are shaped to resemble a Gabor function. As a result, the overall signal consists of a center frequency and two major sidebands plus only a few significant harmonics of those sidebands. The resulting frequency spectrum may have a Q of less than four, but it is far from a flat spectrum over a considerable bandwidth.

The comparison of the dolphins capabilities and those of a relatively simple radar system are probably not useful. The performance of the dolphin system is probably better than, or at least as good as, state-of-the-art single pseudo-noise pulse radars used in modern stealth weapon systems. While the broad-bin histograms in section 7.2 of Au (1993) are illustrative, they do not show the amplitude and phase relationships between individual components of the sideband information that can be used effectively to recover additional information. Au makes note of the potential of the "elementary signal" defined by Gabor, as the basic function in signal decomposition rather than the conventional sinusoidal function in Fourier analysis. He also presents information on multiple pulse

correlation and rippled waveforms in chapter 4. These concepts suggest the capability of the dolphin system is quite advanced relative to, or equals the performance of, similar man-made systems.

Au suggests on page 137 that acoustic power output levels of 60 watts are achievable in some dolphins.

In light of the generic performance of mammalian hearing, it is likely that the dolphin uses both the envelope detection model and the spectrogram correlation models simultaneously. This will be explored in conjunction with the proposed dolphin echolocation schematic in a following section.

### 1.1.3.2 The external anatomy and beam forming capability of high frequency vocalization

### 1.1.3.3 Typical signaling waveforms of the dolphin

Bullock & Gurevich have provided a useful discussion of dolphin sounds (p. 74-81). A problem has been the infrequent separation of the sounds below 30 kHz into purpose-oriented classes. From a system perspective, the unique swept continuous tone signal should be separated from all of the other quacks, croaks, screams, barks, etc. The timing and other characteristics of this swept waveform clearly indicate it is part of a continuous tone sonar system probably exhibiting a Doppler capability. The other sounds do not suggest such a capability.

It is proposed that all of the sounds generated by the bottlenose dolphin must be separated into three distinct classes; the low frequency (LF) communications sounds, the high frequency (HF) swept frequency sonar sounds, and the ultra high frequency (UHF) pulse sonar sounds. Such a separation provides a different interpretation than the comments of Markov, et. al, and Tomilin in Bullock & Gurevich (p. 76-77). When ranging, the HF whistles are necessarily monotonous because it is their echo that carries information, not the emitted whistle. On the other hand, the LF sounds contain information worthy of recovery by other members of the species. These sounds will be considered elements of the dolphin language, described here globally as Dolphinia. Dolphinia is likely to contain a great many dialects due to the separation of various herds by great distances.

Bullock & Gurevich (p. 87) reference Ayrapet'yants, et. al. as describing the social communications range of the dolphin as 5-10 km.

#### 1.1.3.3.1 Click-type waveforms

The literature contains a great many casual statements concerning the signal parameters associated with dolphins. The term broadband is frequently associated with the high frequency signaling of dolphins. **Figure 1.1.3-4** shows that the analogy is not necessarily appropriate. In this figure, the pulse transmitted at about 130 kHz occupies a bandwidth of less than one-third of the center frequency. Such a signal is generally described as a narrow band signal in engineering disciplines. Thus, the dolphin is capable of generating high power and narrowband pulse signals within a broader range of frequencies (80-150 kHz). This range is still less than 2:1.

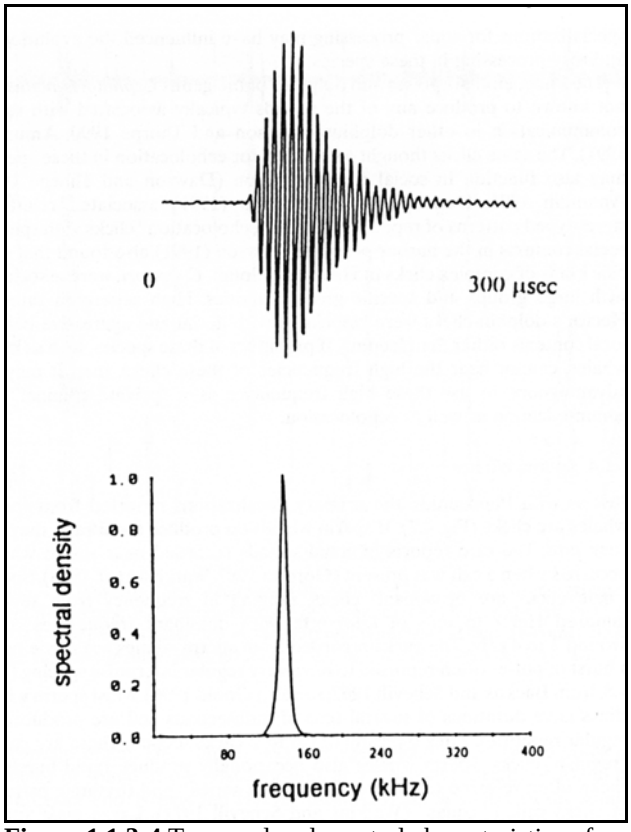


**Figure 1.1.3-4** Temporal and spectral characteristics of a high frequency click. From Tyack & Clark, 2000.

**Figure 1.1.3-5** shows a click waveform measured repeatedly by Lemerande at San Diego. It shows a very good quality single cycle waveform at a nominal 78 kHz. This is truly a narrow band signal with some harmonic content. This click would allow much more precise range and range rate determination (much smaller standard deviations) than possible with the above click from Tyack & Clark.

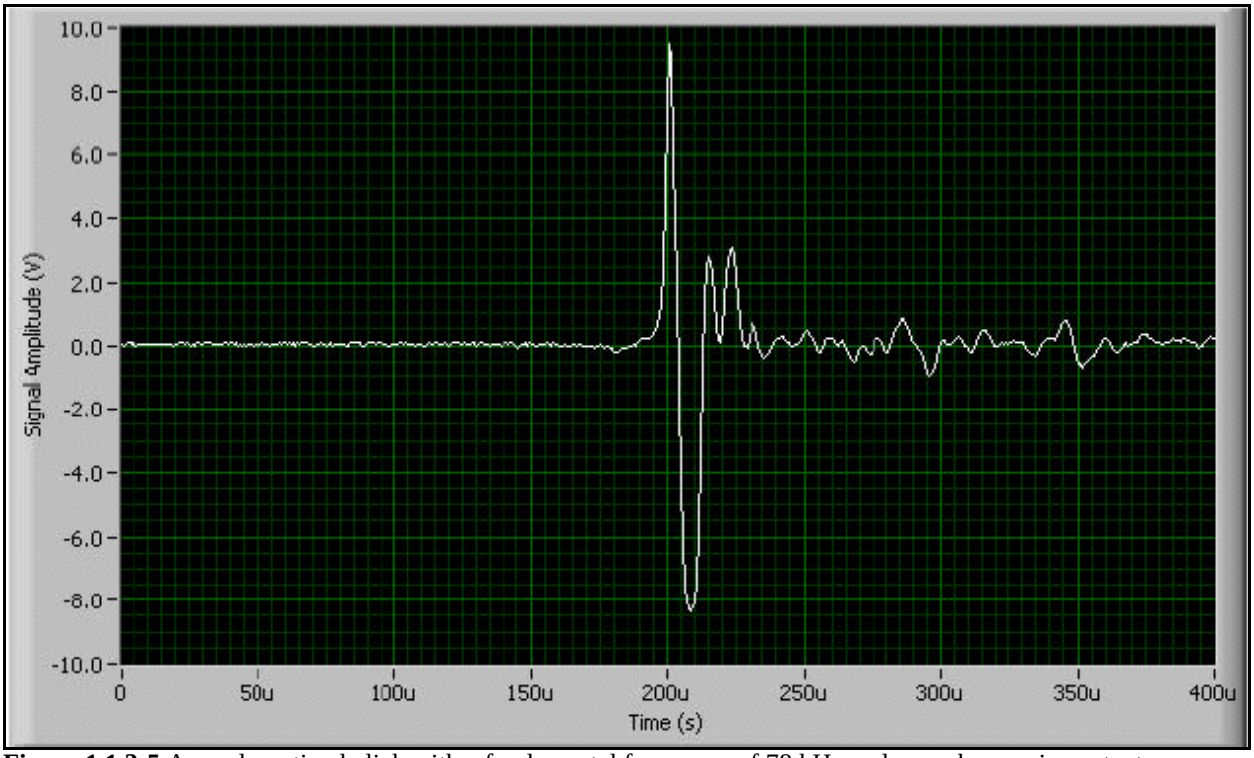


**Figure 1.1.3-5** A nearly optimal click with a fundamental frequency of 78 kHz and some harmonic content (particularly in the after pulse). Energy beyond 230 microseconds is believed to be reverberations within the skull of the animal. From Lemerande, 2002.

### 1.1.3.3.2 Whistle-type waveforms

Many of the following waveforms were recorded under recording system limited conditions with frequencies typically limited to the human audio range. Only recently has Kassewitz implemented a single system that can record from a few hundred cycles to 150 kHz (**Section 1.7.1**).

The spectral waveforms representing dolphin sounds are extensive but not easily comparable. The range of sounds produced is great and the variation in the sequence of these sounds is also considerable. **Figure 1.1.3-6** reproduces a typical low frequency spectrum presented by Sayigh (Reynolds, p. 77). This figure shows considerable harmonic content within a single emission.

The low frequency "whistle" sounds are usually described (Cranford, 2000, p. 111) as "generally narrow bandwidth, often frequency modulated, sounds that commonly last from half a second to a few seconds and may have harmonic structure. Such whistles have been observed at depths of 300 meters, but with changed duration and frequency composition."

The ability of *Cetacea* to make significant sounds at great depth (an area not generally visited by dolphins) remains an area of research. Cetacea can be described as "breath holders." As a result, the air in their pneumatic passages is greatly compressed when diving, to the point that their rib cages are designed to collapse at depth. As a result, the available volume of air at depth is negligible compared with the surface volume. There has been speculation that nearly all of the air from the lungs is transferred to the nasal sacs to allow continued echolocation at great depths[75]. In the case of the bottlenose dolphin, soundings at depths exceeding 200 meters have been reported.

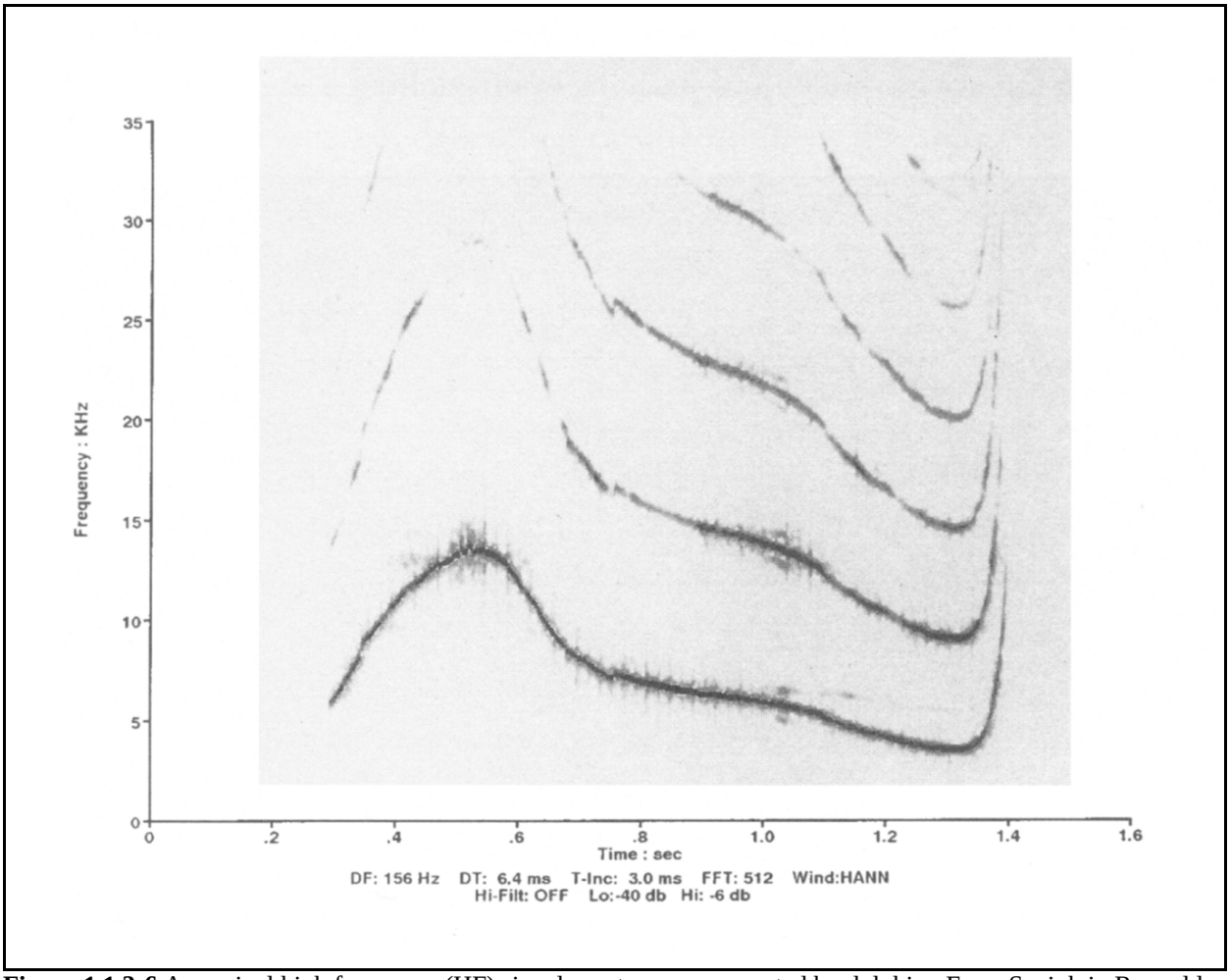


**Figure 1.1.3-6** A nominal high frequency (HF) signal spectrogram generated by dolphin. From Sayigh in Reynolds et al, 2000.

[75]Houser, D. Finneran, J. et al. (2004) Structural and functional imaging of bottlenose dolphin (Tursiops truncatus) cranial anatomy *J Exp Biol* vol 207, pp 3657-3665

**Figure 1.1.3-7** shows an alternative and more extensive set of spectrograms from Caldwell et al[76]. These recordings display almost no harmonic content. The reason may relate to equipment capability. Only a few first harmonics (below 12 kHz) of low frequency components are shown. They note the difference in characteristics of the low frequency signals from two different juvenile males. Each individual sequence was labeled a loop in their presentation. They note the repetitive nature of the patterns in each loop. However, they also note the frequent occurrence of an introductory or terminal loop that differs from the central loops (sequence at lower right). The difference in the loop structure between animals provides a significant interference rejection capability when several individuals are hunting in a single pack. Caldwell et al, provide considerable information concerning the variation and stereotypical characteristics of whistles from specific dolphins.

It is very likely that the harmonic content (which may be controllable) of the emitted signals plays a significant role in determining the radial dimension and the internal texture of targets. The harmonic content would be quite useful in distinguishing a real fish from a metal imitation placed in the water by a researcher. For larger specimens, it could help distinguish a real target from a Styrofoam impersonation of uniform density.

[76]Caldwell, M. Caldwell, D. & Tyack, P. (1990) Op. Cit.

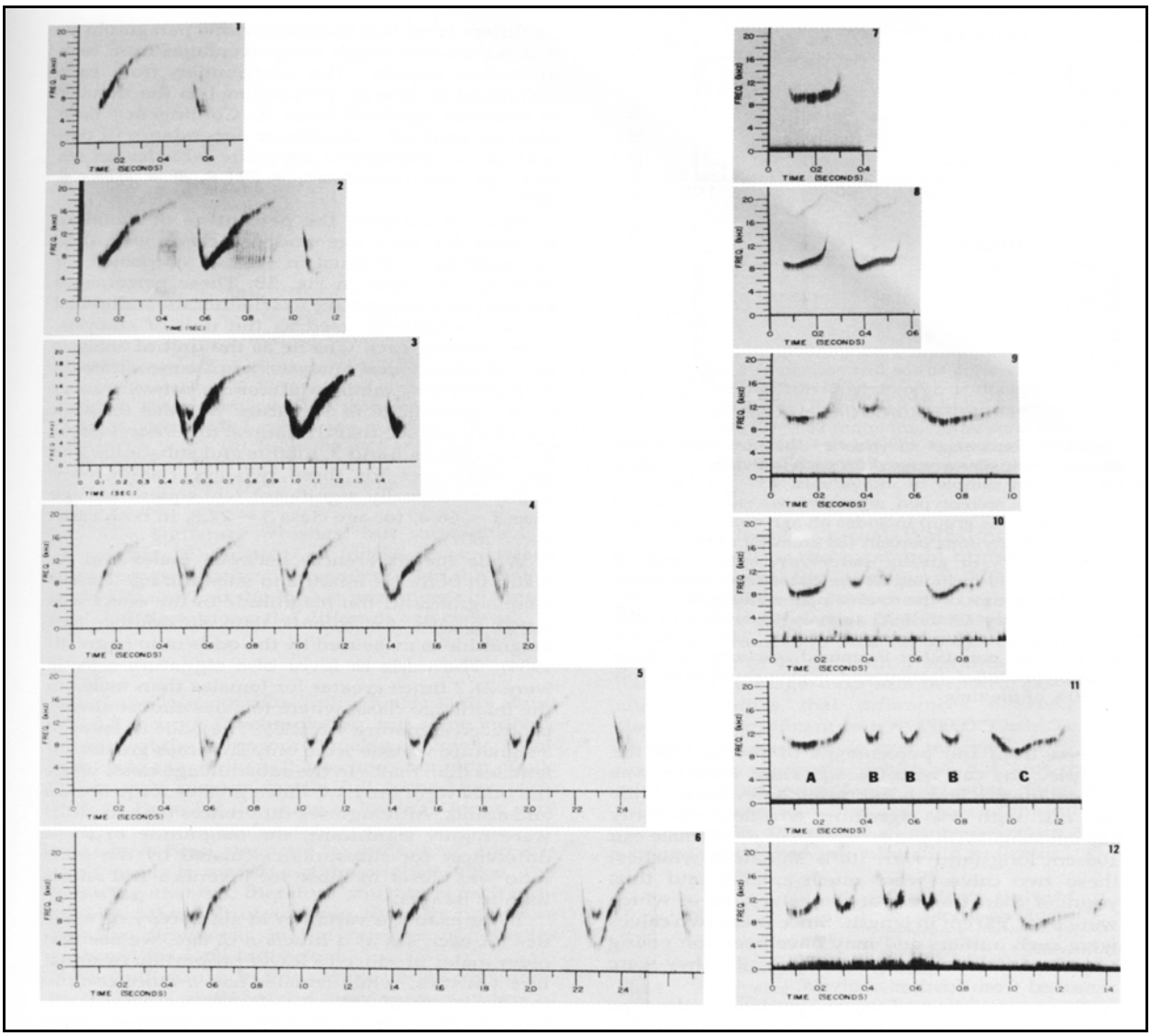


**Figure 1.1.3-7** A collage of LF spectrograms from two Atlantic bottlenose dolphins. The frequencies are below 20 kHz. Left; one to six loops of a juvenile male. Right; one to six loops of a different juvenile male. Note the labeling, A, B, B, B, C at lower right showing variations in the loops of one sequence. From Caldwell et al, 1990.

Caldwell & Caldwell had earlier described the whistles of 126 infant-to-young Atlantic Bottlenose Dolphins during their development[77].

### 1.1.3.3.3 Truncatus waveforms recorded in the Sado estuary of Spain

Santos, et. al. have identified a wide range of whistles recorded in the Sado estuary near Lisbon

[77]Caldwell, M. & Caldwell, D. (1979) The whistle of the Atlantic Bottlenosed Dolphin (*Tursiops truncatus*)–Ontogeny *In* Winn, H. & Olla, B. *eds*. Behavior of Marine Mammals, Volume 3 Cetaceans. NY: Plenum Press Chap. 11

Portugal from a resident herd of bottlenose dolphins[78]. They attribute these whistles to social communications as much as to echolocation. **Figure 1.1.3-8** reproduces their two tables.

[78]Santos, M. Caporin, G. et. al. (1989) Acoustic behaviour in a local population of bottlenose dolphins *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pp 585-598

TABLE 1. Whistle characteristics.

| Type | Contour | Frequency (kHz) Minimum | Maximum | Initial | Final | Duration (ms) |
|---|---|---|---|---|---|---|
| AZ | | 5 - 8.5 | 16 - > 16 | 5 - 9 | 8.5 - 16 | 650 - 1500 |
| US | | 4 - 7.5 | 10 - > 16 | 4 - 7.5 | 10 - > 16 | 600 - 1100 |
| SU | | 5 - 6 | 9 - 13 | 5 - 6 | 9 - 13 | 450 - 550 |
| AR | | 7 - 9 | > 16 | 7 - 9.5 | 7.5 - 9.5 | 225 - 325 |
| ME | | 4 - 5.5 | > 16 | 4 - 5.5 | 5.5 - 14 | 950 - 1900 |
| SM | | 4 - 5.5 | 16 | 4 - 5.5 | 16 | 370 - 650 |
| AP | | 3.5 - 7 | 14 - 16 | 3.5 - 11 | 5 - 13 | 600 - 2400 |
| SP | | 6.5 - 7.5 | 11.5 - 13.5 | 6.5 - 8.5 | 7 - 7.5 | 275 - 700 |
| CA | | 5.5 - 8 | 15 - 16 | 5.5 - 15 | 6 - 14.5 | 450 - 700 |
| CM | | 7.5 - 8 | 15 - > 16 | 7.5 - 13 | 9 - > 16 | 350 - 600 |
| SC | | 4.5 - 7.5 | 10.5 - 13.5 | 5 - 13.5 | 4.5 - 7.5 | 475 - 800 |
| DD | | 5.5 - 8.5 | 9.5 - 10.5 | 9.5 - 10.5 | 4.5 - 8.5 | 825 - 1000 |
| SD | | 3.5 - 5.5 | 12 - 16 | 3.5 - 10.5 | 12 - 16 | 550 - 900 |
| AA | | 6 - 8 | 13 - > 16 | 6 - 9.5 | 13 - > 16 | 550 - 1725 |
| CS | | 5.5 - 6 | 14 - 14.5 | 14 | 5.5 - 6 | 775 - 800 |
| PU | | 7.5 - 9.5 | 12.5 - 15.5 | 11.5 - 14 | 9 - 15.5 | 650 - 700 |
| KE | | 3 - 4.5 | 8.5 - 9 | 3 - 4.5 | 4.5 - 9 | 550 - 825 |

TABLE 2. Occurrence of recognized whistles.

| Date | US | AP | SU | CM | SP | ME | KE | CA | DD | CS | AZ | SD | SC | AA | AR | PV | SM |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 25.07.87 | X | X | X | | | | | | | | | | | | | | |
| 26.07.87 | | X | | X | | | | | | | | | | | | | |
| 01.08.88 | | X | | | | | | | | | | | | | | | |
| 24.09.88 | | | | | X | | | | | | | | | | | | |
| 23.10.88 | | | | | | X | | | | | | | | | | | |
| 30.10.88 | | X | | | | | X | X | | | | | | | | | |
| 29.01.89 | | X | | | | | | | | | | | | | | | |
| 16.02.89 | | | X | | | | | | | | | | | | | | |
| 17.02.89 | X | | | | | | | | X | | | | | | | | |
| 25.04.89 | X | X | | | | | | | | X | | | | | | | |
| 07.05.89 | | | | X | | X | | X | | | | | | | | | |
| 14.05.89 | | | | | X | | | | | | X | | | | | | |
| 15.05.89 | X | | | | | | | | | | | X | X | | | | |
| 19.05.89 | | | | X | | | | | | | | | X | X | X | X | |
| 28.06.89 | X | X | | | | | X | | | | | | X | X | | | X |
| 29.06.89 | | X | | | | | | | | | | | | X | | | |
| 30.06.89 | X | X | X | | X | | | X | X | | X | X | X | X | | X | X |

**Figure 1.1.3-8** Characteristics and occurrences of whistles in Sado estuary. The contours suggest either communications or personal signatures as much as they suggest echolocation. From Santos, et. al., 1989.

The Santos team recorded these signals from a boat trailing a herd by about 50 meters. Thus all of the sounds were recorded from a posterior location relative to the emitters of the dolphins. Signals up to 24 kHz, but most up to 8 kHz, were recorded. A variety of spectrograms were provided based on these recorded HF band signals. The variety of whistles in Table 1 and their occurrences in Table 2 suggest several potential purposes;

- swept frequency echolocation with signals coded to specific animals,
- signature whistles identifying individuals and their location within the herd, and
- whistles used in intraspecies communications and not specific to an individual.

The animals were frequently found to form multiple herds traveling separately in the large bay. As a result, whistles identifying the location of individual animals at significant distances would not be unexpected. Similarly, coded swept frequency signals would allow simultaneous echo ranging by multiple animals with interference rejection using matched filter techniques.

Whether such signals are used in communications has been studied for years with less than definitive results. Markov & Ostrovskaya discuss the possibilities using caricature waveforms in considerable detail[79]. They review the history of communications studies of dolphins up to 1989. Tyack presented a repertoire of dolphin whistles in an obscure journal in 1986[80]. There has been little work since then on learning to understand any native dolphin language. Most of the recent activity has involved interspecies communications.

### 1.1.3.3.4 Truncatus waveforms & spectra from the Irish Sea & Shannon estuary

Hickey studied the sounds, in the frequency range from 2.5 to 25 kHz, of several resident groups of bottlenose dolphins[81]. The recorded waveforms were similar to those recorded in Spain. Hickey did not cite the work of Santo et al. or the text by Thomas & Kastelein. He did cite similar work in the Sado estuary reported by Harzen in 1998. **Figure 1.1.3-9** reproduces Hickey's figure 3.2. The top row illustrates the basic forms used to create the designations used in the figure. Letter designations are cascaded to describe the shape of a complete whistle. Hickey provided both his stylized waveforms and accompanying raw spectrograms. He did not address echolocation pulses in his material.

Multiple statistical tests were applied to the data by Hickey to differentiate between different herds. He attributed most of the sounds to periods when the animals were foraging for food. Hickey also discussed a variety of trends in the use of whistles by dolphins. He traced the designation of personal, or signature, whistles and shared, or variant, whistles. The shortness of the majority of these whistles was highlighted. He also discussed the development of dialects between herds and their relative isolation.

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[79]Markov, V. & Ostrovskaya, V. (1989) Organization of communication system in *Tursiops truncatus montagu* *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pp 599-622

[80]Tyack, P. L. (1986). Whistle repertoires of two bottlenosed dolphins, Tursiops truncatus: mimicry of signature whistles? *Behavioral Ecology and Sociobiology* vol 18, pp 251-257

[81]Hickey, R. (2005) Comparison of Whistle Repertoire and Characteristics Between Cardigan Bay and Shannon Estuary Populations of Bottlenose Dolphins (Tursiops truncatus): With Implications for Passive and Active Survey techniques *In fulfillment of a Master's Degree*, University of Wales (Bangor), GB *Copy in WhDolphin folder*

A problem with the Hickey notation is it does not include trills with harmonics present. It is proposed to employ a trailing numeric to indicate the number of harmonics present in a whistle. An example would be an A5 to designate the presence of the fundamental and harmonics through the fifth. The trailing numeric could be a superscript but that would complicate email messages.

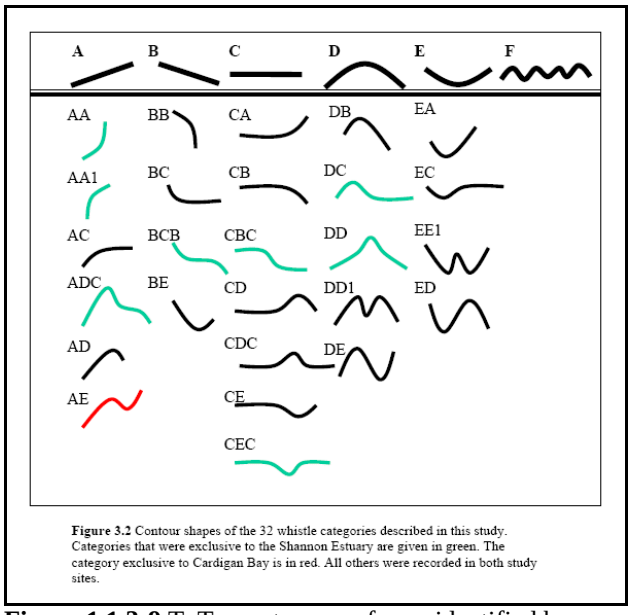


**Figure 1.1.3-9** T. Truncatus waveforms identified by Hickey. From Hickey, 2005.

The conflict between the notation of Santos and Hickey is significant. Both differ from the notation of Taruski for the pilot whale[82]. Markov & Ostrovskaya have presented an entirely different notation. A researcher must be specific as to the terminology followed or introduced. These conflicts highlight two major problems. First, the authors may be speaking of different languages. There is no reason that a pilot whale should be speaking the same language as a bottlenose dolphin. It appears a taxonomy of languages for the marine mammals is needed. While Lilly suggested delphinese for the bottlenose dolphin (page 156), this may not be the best choice of forms. Following the taxonomy of the family, Delphinese should probably be reserved for the language of the family Delphinidae. This could be considered the major language group similar to the designation Romance language includes many subsidiary languages of Western Europe. Tursiopese would be the language of the Genus Tursiops, and Truncatese would be the language of the bottlenose dolphin. Below that would come the dialects described by geographic location. Based on this notation, Markov & Ostrovskaya, Hickey and Santos were studying Truncatese but Taruski was studying Melaenese. If it can be shown that all members of Tursiops can understand each other, the proposed Truncatese language can be demoted to the status of a dialect.

Second, most of the above authors have not provided a statistical study of the frequency of occurrence of each sound. Only Markov & Ostrovskaya have collected enough sound samples to provide a reasonable frequency of occurrence table. Only with such a table is it possible to begin attempting to decode the meaning of these sounds or groups of sounds.

Hardy Jones discussed the findings of Ken Balcom concerning the Orca of Vancouver Island[83]. Balcom has described three distinct dialects for the three pods of Orcas that he has been tracking for many years.

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[82]Taruski, A. (1979) The whistle repertoire of the North Atlantic pilot whale (Globicephala melaena) *In* Winn, H. & Olla, B. *eds*. Behavior of Marine Mammals, Volume 3 Cetaceans. NY: Plenum Press Chapter 10 pg 347

[83]Jones, H. (2005) The Dolphin Defender. Video on PBS, Nature series

### 1.1.3.3.5 Truncatus waveforms from Djurpark, Sweden

Fripp has presented a thesis study of the bottlenose dolphins in Kolmardens Djurpark, Sweden[84]. The goal was to explore infantile vocal development. The work focused more on social and behavioral aspects than it did on presenting waveforms. The recorded bandwidth was from 2 kHz up to "around 30 kHz" using a PAL/VHS recorder. The spectrographic conversion equipment was limited to 32 kHz. All of the waveforms found in this thesis were below 20 kHz and most were below 15 kHz. Time warping was used in this study to compare whistles having different time durations. Using an event sampling approach, over 20,000 whistles were recorded.

Interesting information on the predominance of bubble-stream whistles among calves is provided.

### 1.1.3.3.6 Truncatus waveforms from Sarasota Bay, Florida

Watwood has recently completed a large study of paired dolphins in Sarasota Bay[85]. She identified 125 distinctive whistles within the frequency range between 3 kHz and 20 kHz. She identified a large group of these as associated with signature whistles. Figure 3.1 shows a selection of these signature whistles. She also identified the whistles most commonly shared among pairs of males. No effort was made to associate these whistles with any fricatives within the same frequency band that might lead to an understanding of more complex morphemes. Many repetitions of the same whistle were recorded (with or without brief pauses between them). No harmonic content was presented. No analysis of harmonic contents was provided. A combination of human and automated comparisons were made between the different whistles. The duration of the whistles was not a major consideration in this study. Figure 2.1 does provide some time information. Individual whistles tended to be 300 to 500 ms long.

### 1.1.3.3.7 Characteristics of tonal vs Stressed languages

The majority of human languages are divided into two large groups, the tonal and the stressed languages. While most Indo-European languages are stressed, Chinese, Norwegian, Swedish and many others are tonal in character. These terms apply to individual words within the language. While many languages use variations in tone within a sentence to describe emotion, emphasis and contrast, the use of such variations within a word indicate differences in lexical meaning.

In general, both tonal and stressed languages mature into a form containing both consonants and vowels. While languages consisting of only vowels or only consonants are known, they are rare and generally of limited scope. The written forms of both early Hebrew (Aramic) and Arabic began as consonant only languages.

The spectrograms of Dolphinia (or Truncatese) strongly suggest it contains a component analogous to a tonal language. On the other hand, the spectrograms also show the dolphin makes many staccato sounds that are suggestive of a stressed language. The consequences of these situations will be addressed more completely in a separate appendix.

Amy Stafford has provided a brief tutorial on tonal languages at the website,

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[84]Fripp, D. (1999)

[85]Watwood, S. (2003) Whistle use and whistle sharing by allied male bottlenose dolphins, Tursiops truncatus. Ph D. Thesis MIT/WHOI 2003-14

http://www.mnsu.edu/emuseum/cultural/language/tonal.html . It includes the standardized marks for indicating tonality.

Table 1 -
Common Tone Features[86]
high [ / ]
mid [ - ]
low [ \ ]
rising [ _/ ] (note underline)
falling [ -\ ]
fall-rise [ \/ ]

The use of these marks and the results of using them is shown below for one dialect of Chinese.

Table 3 -
Mandarin Tone Use[87]
Word Intonation Meaning
ba [/] to uproot
ba [--] eight
ba [\/] to hold
ba [\] a harrow

Stafford concludes with;

"As has been shown, there is tremendous diversity in the way that different languages around the world are spoken. Using the same speech features, they are each able to create their own unique way of communicating."

Deutsch & Fodermayr have provided a selection of spectrograms of singing and chanting in various languages around the world[88].

This level of variation with geographic location suggests a similar problem with Dolphin languages/dialects.

### 1.1.3.3.8 Mimicry by dolphins

Richards et al. described the wide range of waveforms that the bottlenose dolphin can mimic in the 200 to 30 kHz range when trained[89]. The range of waveforms goes well beyond the class of waveforms required for effective echolocation. **Figure 1.1.3-10** illustrates this capability. The animal did have difficulty interpreting and reproducing a square wave in frame ( C). It did better in

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[86]Katamba, F. (1989) An Introduction to Phonology. London: Logman Group UK Limited pg 53

[87]Catford, J. (1988) A Practical Introduction to Phonetics. Oxford: Clarendon Press pg 183

[88]Deutsch, W. & Fodermayr, F. (2004) Visualization of Multi-Part Music (Acoustics and Perception). Http://www.kfs.oeaw.ac.at/fsf/mus/Poly1.htm

[89]Richards, D. (1986) Dolphin vocal mimicry and vocal object labeling *In* Schusterman, R. Thomas, J. & Wood, F. *eds*. Dolphin Cognition and Behavior: A Comparative Approach. Hillsdale, NJ: Lawrence Erlbaum Associates Chapter 13

frame (I). The animal shifted the frequency of its response in frames (G) and (H). The ability to mimic a variety of signals from another dolphin goes a long way in supporting the view that dolphins carry out communications using a language learned from their compatriots. While attempts to teach a syntax to the dolphin have not been as fruitful, it is not obvious that a language must have a syntax. Simple pattern matching may be adequate in a language of limited scope.

The dolphin began to mimic the waveform within a fraction of a second, usually around one-third of a second. It is a rare human who can mimic another person with a delay of less than one second.

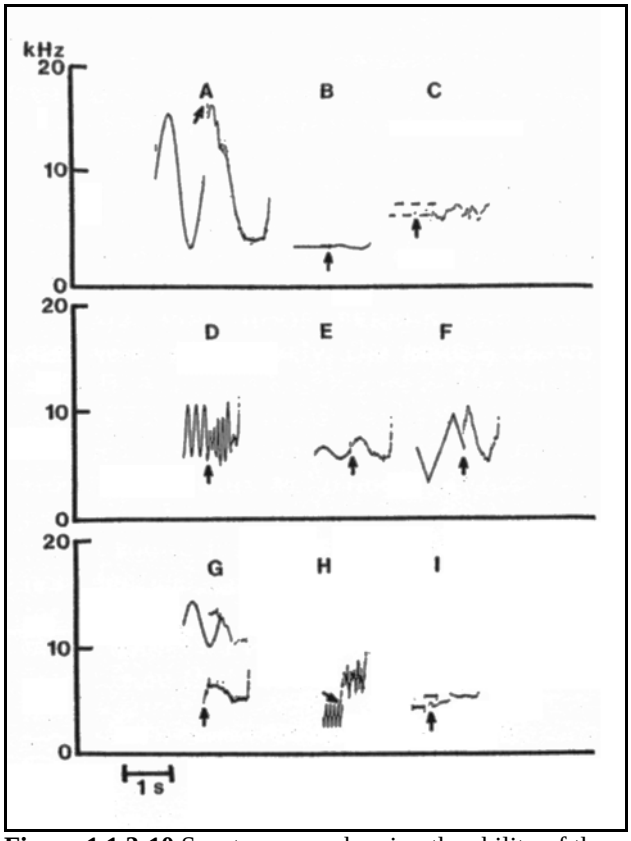


**Figure 1.1.3-10** Spectrograms showing the ability of the dolphin to mimic a synthesized tone. The synthesized signals are to the left of the arrows. The responses typically begin before the synthesized signal is completed, after about one-third second following the start. From Richards et al., 1984

### 1.1.3.3.9 The concept of an individual dolphin adopting a personal noun, limited to a signature whistle

A vibrant debate has been going on since the year 2000 concerning whether the sounds of a given dolphin contain a signature whistle identifying that individual. Some argue that the potential signature whistle may apply to a group but not an individual. Others consider a personal designation unnecessary within the social contexts they have studied. A recent paper has considered a hierarchal general signature whistle for the group with a possible suffix for the individual[90]. That paper disparaged any such whistle and took the view that the lexicon of the dolphin was much to broad to allow isolation of a single signature whistle until more was known about the grammar and semantics of the dolphin. Barton has provided a very recent contribution to the subject and included all of the pertinent references[91].

A second scientific investigatory path was introduced by McCowan, Hanser & Doyle in 1999[92]. It began the study of the sounds of dolphins from the perspective of information theory. While the laboratory portions of these studies have also been limited to less than optimum frequencies and only whistles, the data clearly shows two major features. It shows the breadth of the possible whistle signals is much larger than addressed in the

[90]McCowan, B. & Reiss, D. (2001) The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations *Anim Behav* vol 62, pp 1151-1162

[91]Barton, R. (2006) Animal communication: Do dolphins have names? *Cur Biol* vol 16(15), pp R598-R599

[92]McCowan, B. Hanser, S. & Doyle, L. (1999) Quantitative tools for comparing animal communication systems: information theory applied to bottlenose dolphin whistle repertoires *Anim Behav* vol 57, pp 409-419

above endeavors. It also shows the potential for non-whistles signals within a larger repertoire.

In the context of this work, all of the discussions related to signature whistles has been based only on the whistles (vowel portions) of the dolphin auditory repertoire. Most of the records of these whistles have been truncated to the region below 20,000 Hz by using recording equipment designed for human sound recording. Since the non-echolocation portion of the dolphin auditory spectrum extends up to at least 30,000 Hz, the data recorded to date is analogous to early human telephone communications where the passband of the system was 2,500 Hz or less (as opposed to modern 3,000 Hz telephone channels). Such telephone systems were adequate for message transmission but not for source recognition. This analogy would suggest wider band recordings may show that dolphins can recognize each other by the timbre of their voices without the need of a personal noun. Information theory suggests the auditory and cognitive capability of the dolphin can support a much broader language than that based only on whistle sounds. It would be startling if this additional capability was not used. Physiology suggests the dolphin brain operates using a "frame time" on the order of 30-50 ms. It would also be quite startling from the perspective of information theory if a dolphin should use a minimum duration phoneme of 300-500 ms when it has a capability to interpret auditory symbols at a rate ten times higher. Kasselwitz is now recording dolphin sounds up to at least 80,000 Hz on a relatively continuous basis. These recordings show many harmonic relationships and nuances not recognizable from lower frequency recordings. They also show a wide range of staccato sounds intimately intermingled with the occasional whistle. Both the staccato (consonant) and whistle (vowel) sounds show structure compatible with a 30-50 ms phoneme duration.

## 1.2 The detailed description of the echolocation and communications system of the dolphin

### 1.2.1 The acoustic energy generating capability of the dolphin

The dolphin family can generate at least three distinct signaling waveforms. However, the source of the sounds associated with these classes of waveforms is not completely decided.

- The UHF energy appears to be generated by a mechanical percussion associated with the phonic lips.
- The complex vocalizations at low frequency (LF), including the mimicry noted above, may originate in the larynx (as a broad band noise like source) with energy selection by the structures of the nasal passages. This procedure would mimic communications oriented phonation in other chordates.
- The swept continuous tones associated with the HF signals may be generated in the larynx ***or*** by the phonic lips of the nares. This question remains open because of the scarcity of available data on this subject.

When generating acoustic energy for echolocation purposes, the energy efficiency associated with the conversion of DC energy to AC energy is obviously a major factor in maximum range. However, in an overall echolocation system, the usual quality criteria is energy efficiency per bit of information retrieved. This latter criteria is likely to play a role in separately defining the performance of the HF (swept tonal) and the UHF (pulse) systems.

The water pressure acting on the breath-holding dolphin plays a major role in determining the pneumatic performance of the dolphin's system at significant depths. This factor must be considered when evaluating the dolphin's overall acoustic generation capability.

#### 1.2.1.1 Low frequency sound generation in dolphins RESERVED (<30 kHz)

For now, the LF sound generation capability of the dolphin will be considered as analogous to that of other chordates and involve the larynx.

Popper has provided a valuable table of the sound emissions from selected *Odontocete* species that includes citations[93].

### 1.2.1.2 Ultra high frequency sound generation in dolphins (>100 kHz)

The generation of pulse-type UHF sound has been observed most closely in dolphins. However, the intrinsic methods of sound generation and the characteristics of the sound produced were obscure until the last decade. It is now clear that the UHF energy is generated by the phonic lips. As noted briefly in **Section 1.1.2**, Aroyan has suggested the UHF signals in dolphin are generated in analogy to the LF sounds of other chordates. He suggested a broadband noise source followed by a frequency selective filter followed by a beam forming radiator. This arrangement is conceptually very inefficient energy-wise since much of the energy from the source is suppressed or ignored in the phonic formation process. An alternate description of the process might be conceptually more satisfying. Replace the broadband noise source (a random broadband spectrum) with an impulse generator (a correlated broadband spectrum).

An impulse source can be described as a percussion driven source. A percussion source could be used to excite a resonant structure very efficiently (as a clapper excites a bell). This approach would not use the pneumatic passages of the nares as a resonator. Instead, the pneumatic pressure difference available would be used to actuate the percussion element. The percussion element would excite a tissue structure acting as a resonator. The energy could then be transferred to the radiator efficiently since the radiator would also be tissue based.

The following is offered as a hypothesis. It appears to be compatible with the physical conditions present in the dolphin.

> If the contact points of the phonic lips are calcified and supported by a liquid crystalline support structure connected directly to the melon, the slamming together of the phonic lips could generate a significant resonance in the liquid crystalline support structure. The precise frequency of this energy would be determined by the physical dimensions of the container supporting the liquid crystalline material. In the absence of any structure attached to this material and forming the melon, liquid crystalline materials are known to exhibit very high Q's. They will oscillate for long periods of time with negligible attenuation.
>
> Under the above hypothesis, the rise time of the generated UHF energy would be controlled by the physical characteristics of the percussion element and the liquid crystalline material. This combination is likely to form a second order physical system and the energy as a function of time is likely to exhibit an S-shaped leading edge. If the acoustic coupling between the resonator and the melon is considered tight, the energy of the liquid crystalline material will be rapidly transferred to the melon for projection into the water. This will result in a rapid decline in the energy stored in the resonator. As a result, the energy transferred to the melon and then the ocean will exhibit an S-shaped leading edge followed by a rapidly falling trailing edge. The composite shape of the waveform expected from such action can be expected to look like a Gabor-shaped resonance in the absence of more detailed information.

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[93]Popper, A. (1980) Sound emission and detection by Delphinids *In* Herman, L. *ed*. Cetacean Behavior: Mechanisms and Functions. NY: Wiley Chapter 1

More detailed data would generally show a different time constant for the leading edge of the resultant pulse compared to the trailing edge (leading to an asymmetrical pulse shape shown in the next figure).

As generally accepted, a Gabor shaped pulse is of maximum value in the operation of a background noise limited monopulse echolocation system. It can be used equally efficiently in a multi-pulse train system where additional information may be extracted from the pattern of the echoes received.

Herman has provided samples of spectra from the ultrasonic pulses from a variety of dolphins suggesting the pulses are not ideally shaped Gabor pulses[94]. A specific spectral shape may in fact be diagnostic of a particular dolphin (See page 120 of Au, 1993). However, unlike a finger print, it may be affected by other operating or emotional conditions (including angle between the acoustic receiver and the centerline of the head of the dolphin.

Popper, writing in Herman, incorporated a set of temporal and spectral waveforms from Au of 1974 with only limited interpretation of the Au waveforms and text. Tyack also incorporated some of the Au material without adequate interpretation[95]. A clearer understanding if the reader examines the original paper by Au of 1974 and understands the instrumentation of that period was poor compared to that of today. Popper compared the Au waveforms and later waveforms of Kamminga (1988) in **Figure 1.2.1-1** [96] Note the asymmetrical shape for both the left and right temporal waveforms suggesting different attack and decay time constants. Note carefully the asymmetry n the envelope of the frequency spectrum on the right. It is not a simple Gabor function. as might be assumed. The original Kamminga paper is much clearer concerning the character of the frequency spectra of dolphins, many containing elements of the low frequency portion of the waveform introduced when pulse trains are involved[97]. The volume by Nachtigall & Moore is an excellent resource on animal sonar (about 75% on bat sonar) although it is dated because of the limited recording technology of that day as noted by Kamminga in an addendum on page 21.

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[94]Herman, L. (1980) Cetacean Behavior: Mechanics and Functions. Malibar, Fl: Krieger Publishing Co. page 7. *Reprinted 1988* Also in Au, W. (1974) *JASA* vol 56(4), pp1280-1290

[95]Tyack, P. (2000) *In* Mann, J. Connor, R. Tyack, P. & Whitehead, H. *eds*. Cetacean Societies. Chicago, Il: Univ. Chicago Press Chapter 11

[96]Popper, A. (1980) Sound emission and detection by Delphinids *In* Herman, L. *ed*. Cetacean Behavior: Mechanisms and Functions. NY: Wiley Chapter 1

[97]Kamminga, C. (1986) Echolocation signal types of *Odontocetes In* Nachtigall, P. & Moore, P. *eds*, Animal Sonar. NY: Plenum Press pp 9-22

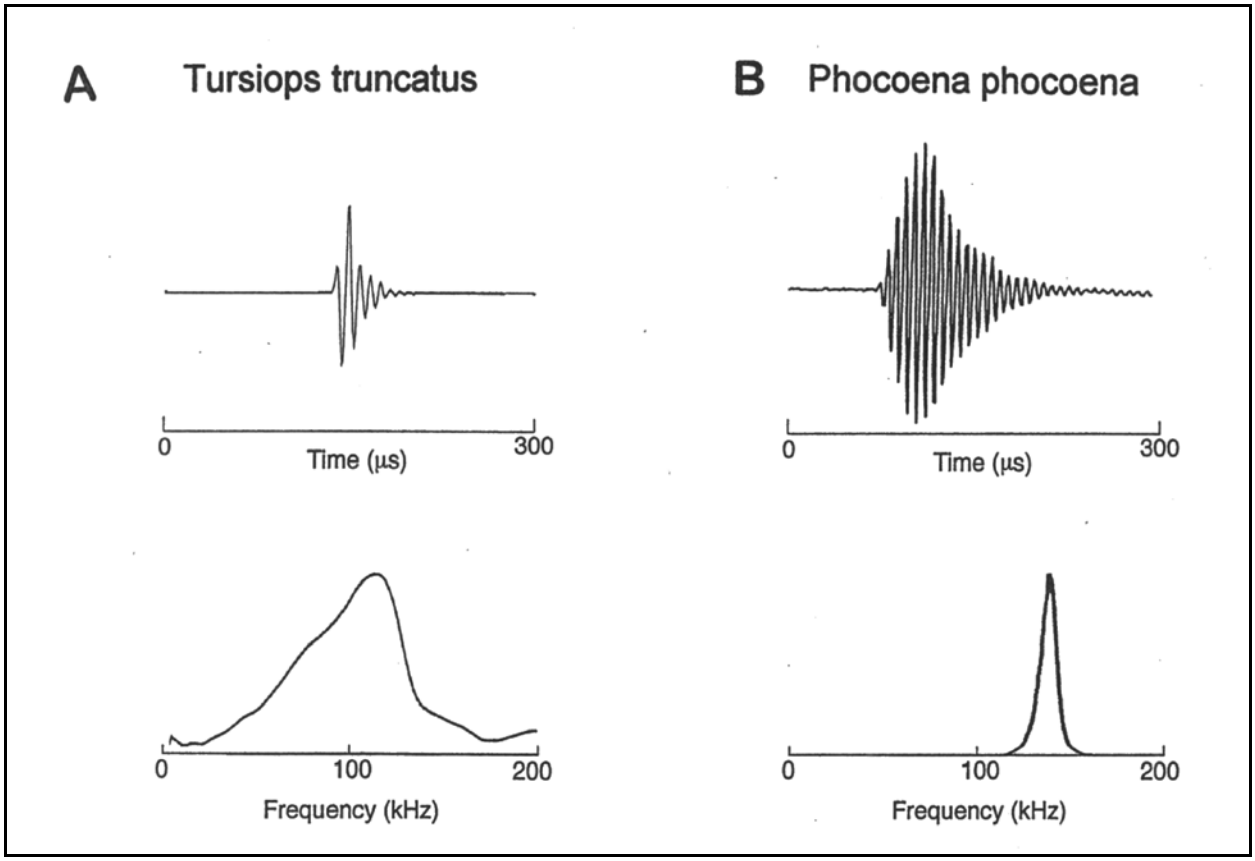


**Figure 1.2.1-1** Temporal and spectral waveforms of "rasp" and "buzz" ADD. Top; temporal waveforms. The *truncatus* waveforms represent the averages of the pulses in an entire click train with variable plse interval, a rasp. The *phocoena* temporal waveform is for a single pulse from a similar pulse train of constant pulse interval, a buzz. See text. From Tyack, 2000; based on Au, 1980 (left) and Kamminga, 1988 (right).

The 1993 book by Au provides copies of his earlier figures and a much more sophisticated discussion of the data acquired concerning the echolocation pulses of dolphins, including a comparison of some individual pulses with the ideal Gabor function[98]. The book also shows the differences in the individual temporal forms associated with far-field pulse patterns recorded at different angles from the axis of the dolphin's head (page 108), presumably from the same intrinsic pulse shape. Pages 78 and 79 appear to present the data behind the left frames of the figure reproduced in Tyack. How the temporal and spectral waveforms were aligned before averaging to obtain a single composite waveform and the variation in intensity of the waveforms was discussed. Au noted the tendency to lose precise information when averaging pulses differing with respect to these parameters. Page 118, although based on Baluga whale data, is indicative of the variation in interpulse group interval that can be expected from a dolphin as well. The results of interpulse variation, the presence of different harmonics with field angle and the limited bandwidth of the recording system (note rise time limit in figure 3) contribute to the smearing of the spectral waveforms traceable to the figures in a 1974 Au et

[98]Au, W. (1993) The Sonar of Dolphins. NY: Springer-Verlag

al. paper[99].

### 1.2.1.3 High frequency sound generation in dolphins (30-100 kHz)

It is difficult to discuss the HF sound generation capability of the dolphin based on the very limited information available concerning the detailed morphology employed. It could be generated using frequency selection associated with a wideband pseudo-noise source as assumed for the LF situation. Alternately, it could be generated as a mechanical resonance as proposed for the UHF system. Another possibility is that it is generated as a conventional pneumatically-based whistle. The multiple large and dynamic air sacs in the head of this breath-holder appears particularly adapted to this role.

Neither the tailored noise source used at LF or the percussion-type resonator proposed for use at UHF are well suited to the generation of swept continuous tones at high power levels. The movement of air in significant volume passed a resonator of the type found in pipe-organs or brass musical instruments appears most appropriate. Of course, the optimum situation is where the energy is concentrated primarily in the tissue medium of the head rather than in the gaseous volumes. Such energy can be transferred from the source to the water most efficiently.

The generation of a swept tone by the larynx appears feasible if air can be transferred back and forth between the sacs of the nares and the lungs. Alternately, the generation of a swept tone by the phonic lips appears feasible if air can be transferred back and forth between the pre-maxillary sacs and the sacs closer to the blowhole ***and*** the phonic lips are compatible with the generation of a continuous tone over a period of a few seconds. The latter approach would require the phonic lips be held rigidly at a very close spacing while the liquid crystalline or other supporting materials were allowed to resonate.

A question arises as to whether the vocal chords of the larynx could be suitable for supporting a vocal range from 200 Hz up to 30,000 Hz, particularly at high power levels and efficiency. An alternate choice would be to use the phonic lips hypothesized above in a fixed configuration in conjunction with the continuous transfer of air. The frequency of the oscillation could by varied by varying the physical dimensions of the liquid crystal also hypothesized above.

Current exploratory research appears to be leaning toward the generation of high intensity HF sound by the phonic lips. The above discussion suggests a common acousto-mechanical mechanism capable of supporting both HF and UHF sound generation.

## 1.2.2 The beam forming capability of the dolphin

The technical literature has made steady progress in defining the beam forming capability of both the transmitting and receiving systems in the dolphin. The progress has been so great that the descriptive literature prior to the year 2000 must be largely discounted. The system is considerably more complex, and of much higher performance, than that referred to conceptually by Au in a poorly timed paper[100] (2004). Both the transmitting and receiving systems incorporate a variety of functional elements and resulting capabilities not considered by Au. The expansion of these

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[99]Au, W. Floyd, R. Penner, R. & Murchison, E. (1974) Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters *J Acoust Soc Am* vol 56(4), pp 1280-1290

[100]Au, W. (2004) Op. Cit.

capabilities explains why the signal processing and signal manipulation capabilities of the dolphin neural system have been expanded so significantly. These capabilities have resulted in a brain approximately the same size as the human brain (in an animal about three times larger in mass) but containing a very different allocation of resources (**Section 1.4.4**).

Bullock & Gurevich reference Ayrapet'yants, et. al. (1969) in describing "some of the features of the system in solving near-threshold discrimination; shorter echolocating pusles (30-150 μsec), changes in the pulse envelope, in the frequency composition, in the number of principal sinusoids in the pulse, and in the modulating sinusoids in the pulse, and scanning head movements which began 7-8 m away from the target. They emphasize that the directionality of the beam can be varied widely and its direction can be rapidly changed without head movement." This is the only strong statement found that would suggest the beam-forming system is as dynamic as modern "track while scanning" radar sets.

The following sections will show the click generating capability involves two distinct and parallel sound generators. The literature reports these generators can be used in synchronism or sequentially with different tone frequencies. Some authors claim these two UHF generators can be used simultaneously with a HF generator.

### 1.2.2.1 High frequency, wide beam, echolocation in dolphins

The operating characteristics of the high frequency (HF) sonar, using a swept tone within 6 to 30 kHz, of the dolphin has not been well characterized to date. In fact, it is not agreed whether the HF signals are generated in the larynx or in the phonic lips of the nares. With this ambiguity, it is difficult to define the beam forming capability of the HF system. Based on the lower frequency, and longer wavelength, of the energy relative to the size of the dolphin, the beam forming capability can be expected to be considerably poorer than for the UHF capability.

#### 1.2.2.1.1 The anatomy of HF echolocation in dolphins RESERVED

#### 1.2.2.1.2 The schematic of HF echolocation in dolphins RESERVED

### 1.2.2.2 Ultra high frequency, narrow beam, echolocation in dolphins

#### 1.2.2.2.1 The anatomy of UHF echolocation in dolphins

**Figure 1.2.2-1** shows the general layout of the echolocation system of the Atlantic bottlenose dolphin, *Tursiops truncatus*[101].

[101]Johnson, S. (1986) Dolphin audition and echolocation capacities *In* Schusterman, R. Thomas, J. & Wood F. *eds*. Dolphin cognition and behavior: a comparative approach. Hillsdale, NJ: Erlbaum Assoc pp 115-136

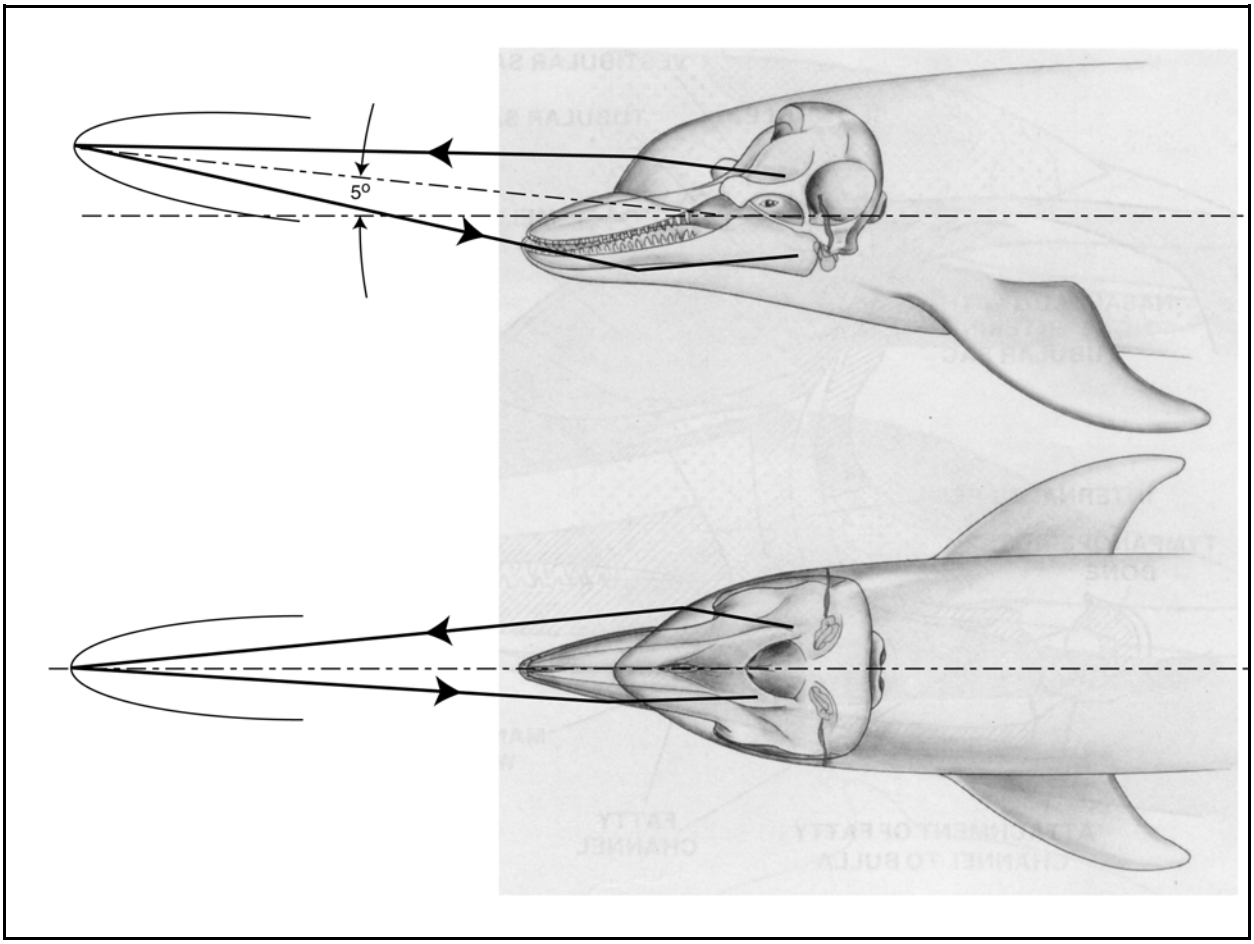


**Figure 1.2.2-1** The echolocation geometry of the bottle-nosed dolphin. The system employs lenses instead of horns to create the radiative patterns used for both echo generation and echo reception. The transmission beam is approximately 10 degrees at the 3 dB point in both planes at 120 kHz. The nominal gain for these angles is 26 dB. The reception beam is slightly broader in both planes at 120 kHz. Modified from Johnson, 1986.

The system has evolved nearly beyond recognition compared to that of other mammals. The anatomical feature commonly called the outer ear is no longer used for hearing but may perform a function akin to a pitot tube in aviation (measuring the relative pressure of the external environment. The energy collected in support of hearing is received through a pair of gradient index Luneburg lenses aligned along the lower jaw. Similarly, the sound source is not in the larynx but in additional structures located between the larynx and the blowhole. Note the external opening of this tube is closed during click generation (and during lower frequency underwater vocalization).

The generated energy is transferred to the water in a narrow beam through a system similar in concept to the lens system of the mammalian eye. This system forms the large structure above the mouth of the dolphin (the melon and the tissue covering the melon). The melon contains a large asymmetrical gradient index lens (Au, p. 88) separated from the exterior environment by a curved surface reminiscent of the cornea in function. This outer surface forms a lens of significant refracting power. This lens also introduces significant bending of the beam in order to create a far-field beam centered directly ahead and about 5 degrees above the centerline of the animal. The formation of the transmitted beam is highly frequency dependent. The pattern can be widened by more than 2:1 by lowering the frequency of the signal to 30-60 kHz. The equivalent aperture of the transmitting

system is a single circular plate of 2.0 to 5.0-cm diameter depending on species.

Only limited data is available on the operation of the lens system. Norris & Harvey have provided data on the velocity of sound through small sections of the melon by dicing it into 1.8 x 1.8 cm x 9.5 cm pieces. Since the wavelengths of interest are as short as one centimeter and field pattern calculations require information at no larger than one-quarter wavelength intervals, this data can only be taken as indicative of the acoustic properties of the lens. They did record velocities that would suggest acoustic indices of refraction on the order of 1227/1500 = 0.818 to 1761/1500 = 1.174 after correction for normal body temperature and taking the speed of sound as 1500 meters/sec under standard ocean water conditions. This wide range of indices, above and below 1.00, would suggest a lens of considerable refractive power, comparable to the lenses of the visual eye (nominal index ranges of 1.45 in acoustics and 1.33 in vision).

The symmetry of the air sac system (and the asymmetry of the connections of the melon to the nares) would suggest a left and right nasal plug. In addition, the imagery of Cranford[102], shown in Au (p. 89) suggests an even more complex interface between each half of the melon and the trachea. These features suggest the transmitting system of the dolphin may employ two phase-related sources in the generation of the overall radiative sound pattern ( a more complex arrangement than characterized by Au on pages 90-91). A pair of phase coherent lateral sources would make horizontal beam formation in the high frequency regime considerably simpler and might introduce additional features well known in the radar and sonar communities.

The receiving system employs a similar acoustic system. The initial components consist of the exterior pliable material directly below each side of the mouth and an interior fatty material controlling the propagation of energy into the region of the acoustic bulla. The energy is delivered directly to a window in the vestibule. This energy traveling as a longitudinal wave is converted into a surface acoustic wave on the surface of the tectorial membrane of the cochlea within the vestibule. As in other marine vertebrates, the dolphin does not require the impedance transforming function of the middle ear. The receiving system can be modeled using an effective collection area of 8.1 $cm^2$ for each ear at a separation of 12 cm.

Au shows the temporal pulse signatures of a series of dolphins on pages 134-135. A typical pulse consists of a Gaussian (or Gaussian-like) pulse of 8-10 cycles followed by one or two pulses of about 4-5 cycles at a lower intensity. The pulse duration is commonly within the typical 30 ms integration time found in many neurological systems. This is a different integration time than used by Au on page 158. That integration time might be more appropriately called a correlation time in the context of this work.

The reflection of a typical signal, as defined above, from a target of variable internal density can be quite complex and the dolphin appears to be able to take advantage of this complexity to identify objects successfully at signal-to-noise ratios greater than 10 dB.

**Figure 1.2.2-2** shows a more detailed lateral view of the dolphin head with its echolocation elements highlighted[103]. It is currently believed that the sound generated by the system is independent of the

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[102]Cranford, T. (1988) The anatomy of acoustic structures in the spinner dolphin forehead as shown by X-ray computed tomography and computer graphics *In* Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pp 67-77

[103]Norris, K. (1968) The evolution of acoustic mechanisms in odontocete cetaceans *In* Drake, E. *ed*. Evolution and Environment. New Haven: Yale University Press pp 297-324

larynx. The sound appears to be generated by the presence of the nasal plug formed by an extension of the melon. This plug vibrates as the result of air being forced passed the plug within the tubular sac. The air is squeezed out of one or more of the various sacs found in this region and received by one of the other sacs. It is believed the air is re-circulated to allow indefinite operation of the system under water. The energy generated at the nasal plug is focused initially by the shape and the gradient index of the material forming the melon. The formation of the beam is completed by the lens formed by the outer skin/water interface. The reflected energy is captured by the window adjacent to the mandibula (lower jaw). This window also acts as a lens in conjunction with the water-to-tissue interface. The captured energy is then focused further and transferred to the area of the tympanoperiotic bone by the fatty channel.

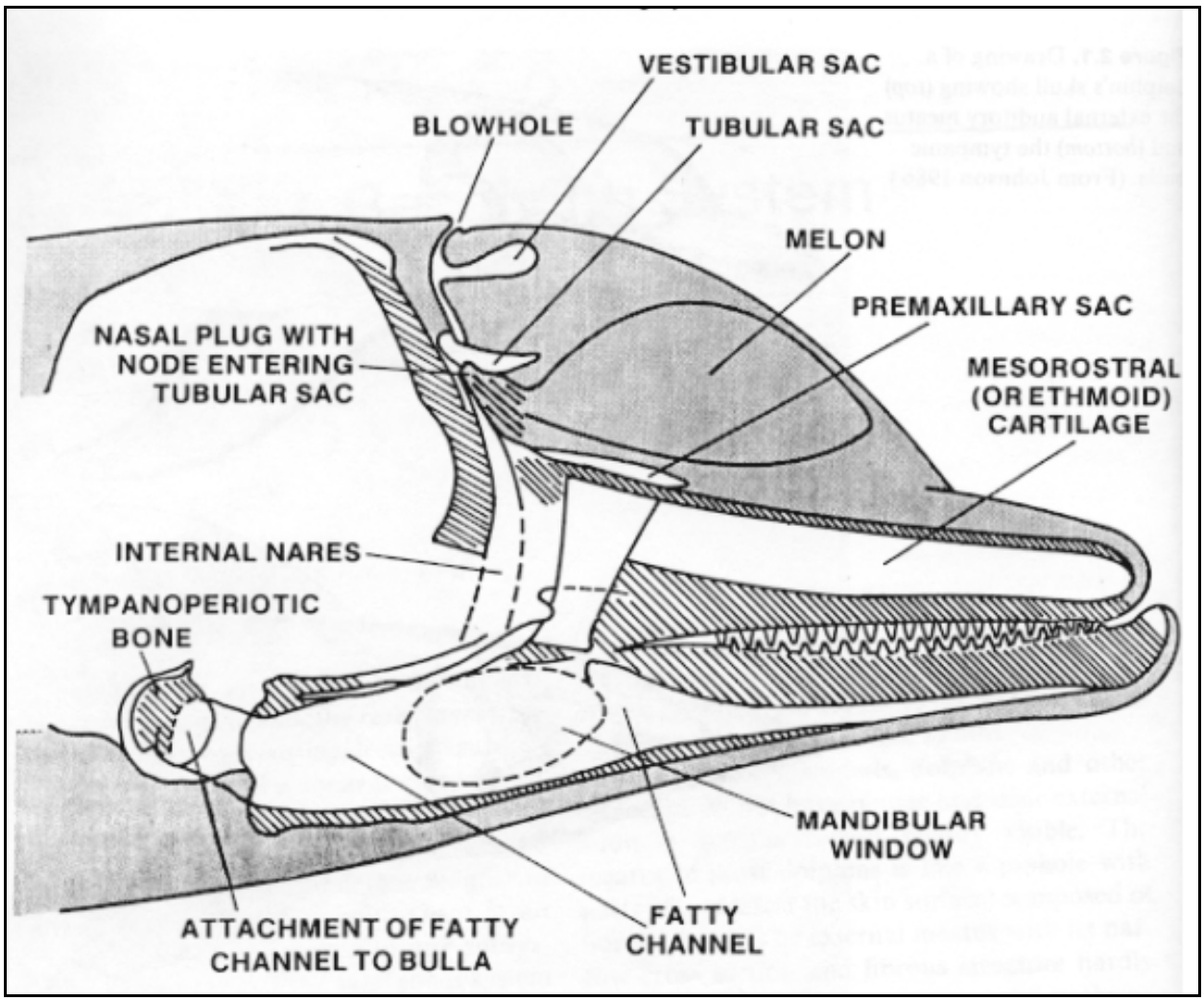


**Figure 1.2.2-2** The general layout of the echolocation system of the dolphin. The fatty cavity forward of the mandibular window is probably not related to hearing. Modified from Norris, 1968.

**Figure 1.2.2-3** shows the overall goal of the UHF energy projection system in profile. A similar figure could be drawn for the plan view of the system.

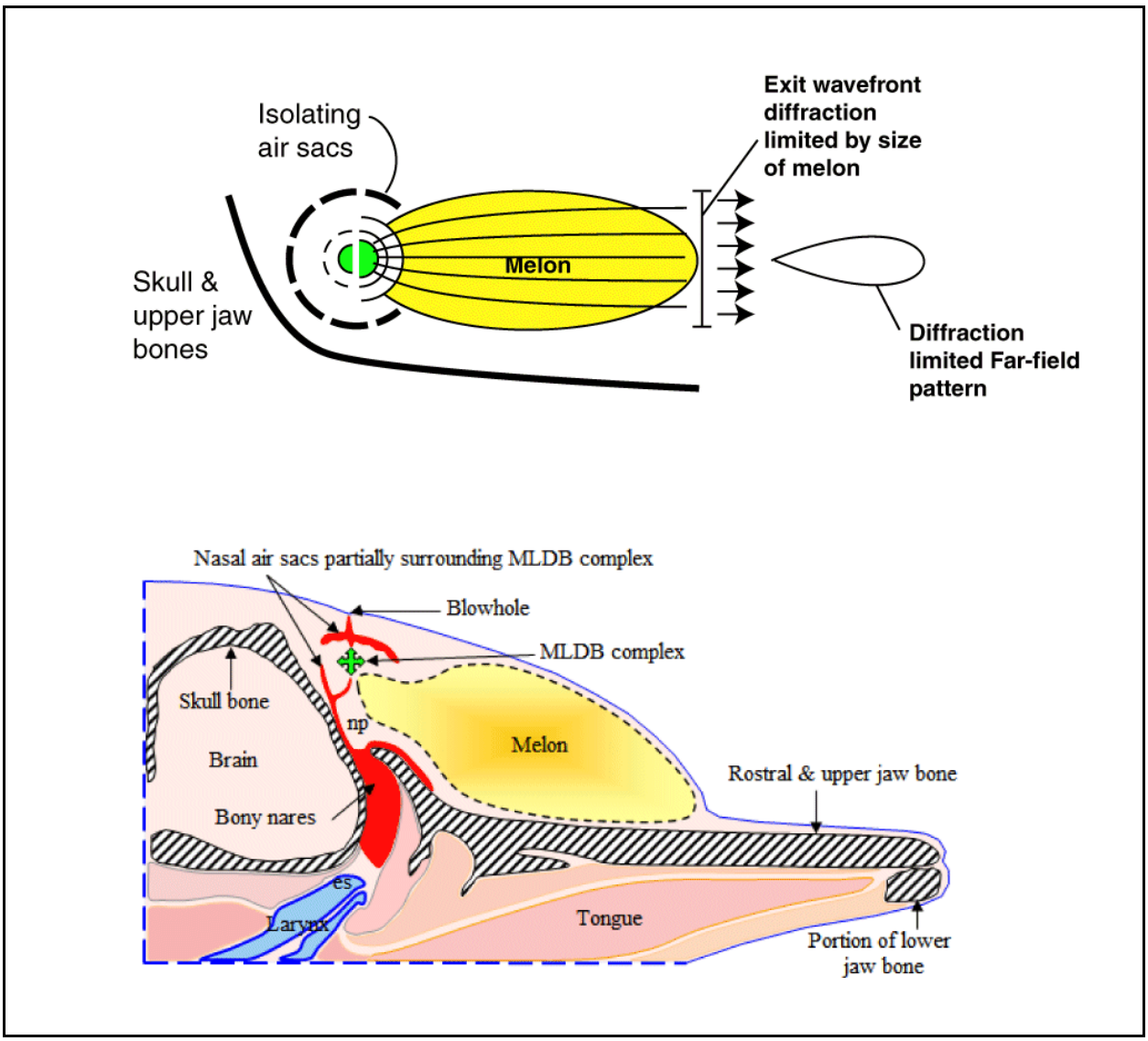


**Figure 1.2.2-3** Conceptual goal of the UHF energy forming system in profile. The object is to forma a uniformly distributed in intensity and parallel in phase wavefront at the effective aperture of the acoustic system in the water immediately forward of the melon. See text. Lower frame from Aroyan, 1990.

The 1993 work of Au (The Sonar of Dolphins, pages 81-114) and the 2002 work of Aroyan http://www2.cruzio.com/~jaroyan/Dolphin%20Model%204.htm provide valuable data for describing the acoustic energy projection system. Arroyan's plus shaped MLDB could be modified to suggest a spherical wavefront more objectively. This is done in the upper frame of the figure. The air passages between the MLDB (or the phonic lips) and the skull are critically important to the operation of the UHF acoustic energy projecting system.

The basic object of the UHF acoustic radiating system of the dolphin is to generate a narrow frequency band high energy signal with a nominally spherical wavefront and convert that into a nominally linear (more accurately planar) wavefront at the exit from the melon. Such a planar wavefront will be diffraction limited in its field pattern by the relationship between the diameter of the aperture formed by the melon expressed wavelengths of the acoustic energy. This diffraction

limited pattern is what is actually measured in the far-field (at least 10 wavelengths from the melon). For discussion, say this beam has a half-amplitude diameter of 10 degrees in both the horizontal and vertical planes.

The UHF acoustic energy is generated initially as a spherical wavefront emanating from the phonic lips within the nares (labeled MLDB by Aroyan). The lips are shown as different in size in the upper frame of the figure to suggest the amount of energy in the forward propagating and rearward propagating wavefronts may be different based on the characteristics of the lips. The energy from the rearward lip is not useful and is either absorbed or reflected by the nasal air sacs labeled the air sacs partially surrounding the MLDB or the vestibular sacs in Aroyan's figures. The goal of the melon, a gradient index lens, is to steer all of the forward projecting energy into a wavefront (on the water side of the melon-water interface) that is planar, of uniform intensity and perpendicular to the direction of projection (shown here as parallel to the axis of the animal). Some variation in the intensity uniformity may be present (apodization in antenna language) and would lead to marginally better far field beam sharpness. However, the research literature has not advanced far enough to identify any such apodization in dolphins.

The ring of isolating air sacs is actually more complex than shown. There are multiple air sacs, each acting as a reflecting surface. By optimally shaping the surface of these air sacs facing the source, attenuation of energy traveling toward the brain and skull can easily exceed 30 dB (and probably 50 dB) *per surface*, think of the F-117 stealth fighter). By reflecting the energy traveling toward the skull into an absorbing area, the side lobe pattern of the overall system can be improved.

Contrary to some illustrations, the skull plays no significant role in beam formation. The construction used in the dolphin head essentially isolates the skull and brain from the energy of the acoustic projection system and insures no significant UHF energy reaches the skull and brain. On a long term basis, UHF energy reaching the brain would have a homogenizing effect and be destructive of the brain.

Although not defending the adequacy of his model, Au has shown by simulation on page 94 that any energy reflected by the skull is effectively lost in the sidebands of the projected beam. With the air sacs added, the beams of page 95 of Au are obtained (credited to Aroyan, 1990).

The energy emanating forward enters directly into the melon tissue (as shown very nicely in Au (page 89). The physical arrangement of the two input points to the melon shown on page 89 of Au are used for high resolution spatial discrimination and are not of interest here. The main point is the energy enters a region of variable acoustic density. The initial spherical energy wavefront is formed into a nominally planar wavefront at the forward surface of the melon. This is the beam forming mechanism in dolphins. While it does not look like a lens, it is in fact a gradient density lens in acoustic optics.

### 1.2.2.2.2 The potential for rapid beam steering

Several authors have described high speed sweeping of the UHF beam of the bottlenose dolphin. Such sweeping could be achieved by several methods. **Figure 1.2.2-4** shows in caricature the ability to change the beam direction based on the asymmetry in the locations of the dual sources of the bottlenose dolphin (See **Section 1.1.2.3.3**). Without detailed knowledge of the location of the sources and the feed structure between the sources and the melon, this beam steering mechanism cannot be demonstrated or quantified. An equally possible method of beam steering involves muscular change in the shape of the melon or the feed structure. A third possible method involves changing the

location and content of the air sacs (acting as mirrors) within the forehead.

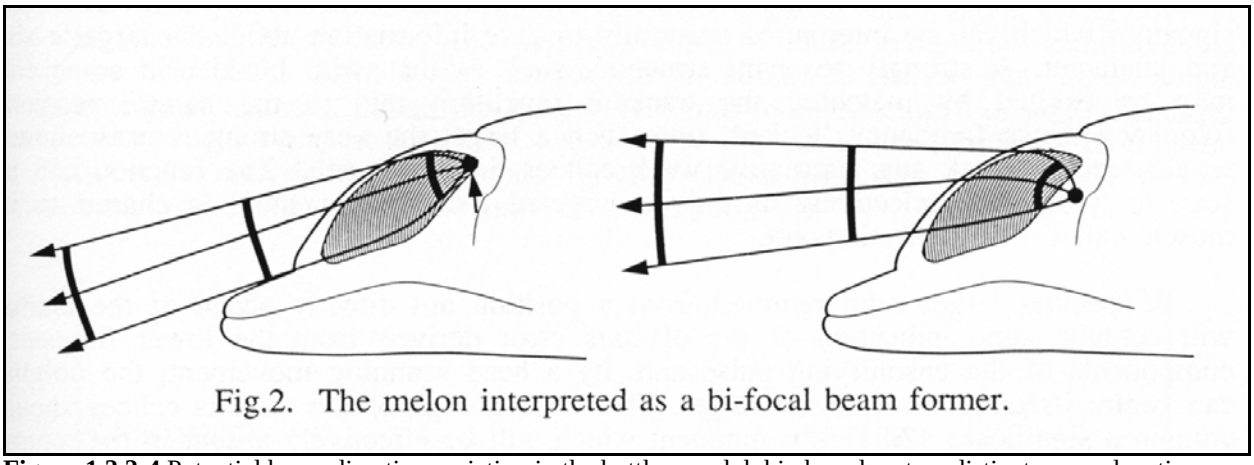


**Figure 1.2.2-4** Potential beam direction variation in the bottlenose dolphin based on two distinct source locations. The sources may also have a lateral displacement that may also affect the beam direction. Potential changes in beam direction/form due to muscle activity are not shown. From Goodson & Klinowska, 1989.

Bullock & Gurevich (p. 74) review some of these possibilities and the remarkably high rate of beam steering reported without documentation by Reznikov. Reznikov claimed the beam could be rapidly rotated at a rate of $3.5 \times 10^5$ degrees/sec independent of any head motion. Such a high rate might be generated by interference between the two sources operating at slightly different frequencies. Such high rates due to muscular action seem unlikely unless the melon is operated in a multi-lens folded telescope configuration.

### 1.2.2.3 Potential operation in the 150-390 kHz

Lemerande has provided some very interesting field research results at frequencies above those explored before[104]. He makes the following assertion. "EFSDLs at 390 kHz clearly show the dolphin has the capabilities to actively use frequencies almost three times higher than previously documented Tursiops Truncatus sound emissions to echolocate a target." This assertion is made entirely on the basis of his recording energy emitted by the dolphin as measured at ranges of a few meters. He did not consider the two-way attenuation of the signals or the operation of the dolphins auditory system.

## 1.2.3 The range measuring capability of the dolphin

Murray, Mercado & Roitblat provided a simple computational model describing the ranging capability of the false killer whale[105]. Although they do not introduce a feedback loop within the

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[104]Lemerande, T. (2002) Transmitting beam patterns of the Atlantic Bottlenose Dolphin (*tursiops truncatus*):
Investigations in the existence and use of High frequency components found in Echolocation signals. Naval Postgraduate School, Monterey, CA 93943-5000

[105]Murray, S. Mercado, E. & Roitblat, H. (1998) Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations *J Acoust Soc Am* vol 104(3), pp 1679-1688

auditory system, Murray's team offered a number of useful observations concerning the sounds emanating from the false killer whale. They noted the ability of the animal to generate both continuous tones and simultaneous pulses within the frequency range below 22 kHz. They also noted that when the animal generates a series of pulses with spacing of less than 5 ms, humans perceive this signal as a continuous tonal sound.

A key feature of ranging by marine mammals appears to be the overlap between the pulse transmitted and the received signal as an echo from the previous pulse within the inferior colliculus. This time coincidence allows the animal to adjust the pulse-to-pulse interval to center the next transmitted pulse relative to the echo. This adjustment can be made on a pulse-to-pulse basis. As a result, the pulse-to-pulse interval of the pulse generating system (averaged over several pulses) is directly proportional to the distance of the target from the animal. This signal is produced by a simple servomechanism without any counter circuits or complicated correlation calculations.

Not many investigators have focused on the relative time between the receipt of a ranging echo and the time of generation of the next output pulse. To measure this feature requires specialized test equipment and a detailed knowledge of the physiology of the animal involved.

Novick has analyzed the pulse overlap characteristic in the ranging servomechanism of the bat, *Chilonycteris parnellii*[106] *and Chilonycteris psilotis*[107]. All phases of the search, pursuit and capture (terminal) sequence are discussed.

The multiple air chambers in the head of the dolphin and the isolation of the cochlea within bulla isolated from the skull are very effective in isolating the high power transmitting capability of the dolphin from the high sensitivity of the receiving system. This isolation is further supported by the location of the beam-forming melon above the aural cavities and the two beam-forming receiving structures below the aural cavities.

### 1.2.3.1 The related range measuring capability of the bats

Although the repertoire of techniques used by the bats differ in some aspects from those used by *Cetaceans*, a comparison is appropriate.. In some cases, such a comparison offers additional insight into the physiology and capability of *Cetacea*.

The very detailed data provided by the Novick team is typified by **Figure 1.2.3-1**. The portion of the figure to the right of the arrow relates to the acquisition mode of the bat. The time from the arrow down to 125 ms represents the pursuit phase. The terminal phase begins at 125 ms. These phase designations differ slightly from Novick as discussed below. A problem appears in the caption of most of their figures. They provide the expression "One msec = 1.73 mm." This should be " bat movement during 1 msec = 1.73 mm." or "bat flight speed = 1.73 mm/ms" as given in their Table 1. The round-trip travel time for an acoustic signal is 100 times higher at 170 mm/ms. Based on their assumption of a constant bat velocity during their recording sequences, an auxiliary scale has been added to the left of the figure. This scale suggests that these bats, like other species, depend on the sounds made by their targets for locating food at ranges exceeding one meter. Thus, the bat's search mode uses passive sonar while the acquisition, pursuit and terminal phases of the predation mode uses active

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[106]Novick, A. & Vaisyns, J. (1964) Echolocation of flying insects by the bat, *Chilonycteris parnellii*. *Biol Bull* vol 127, pp 478-488

[107]Novick, A. (1964) Echolocation of flying insects by the bat, *Chilonycteris psilotis*. *Biol Bull* vol 128, pp 297-314

sonar. This situation suggests this bat uses the characteristic sounds of its prey to classify its targets during the search mode. The data clearly shows this bat uses a variety of swept frequency pulses during the initial acquisition, the pursuit and the terminal phases of an encounter.

Novick speculates that the bat may use a servomechanism based on pulse overlap to determine the range to the target on page 307. He notes this technique is independent of the speed of sound and does not require the ability to discriminate short intervals of time. This bat used a fundamental tone of 21 kHz plus the $2^{nd}$, $3^{rd}$ and $4^{th}$ harmonics. "Either the second or, more often, the third harmonic is at the highest amplitude, especially during the terminal phase (Fig. 1)." Pulse to pulse frequency stability appears to be better than 1 kHz. Intra-pulse, the tone frequency drops from 21 to 17 kHz in a generally linear sweep.

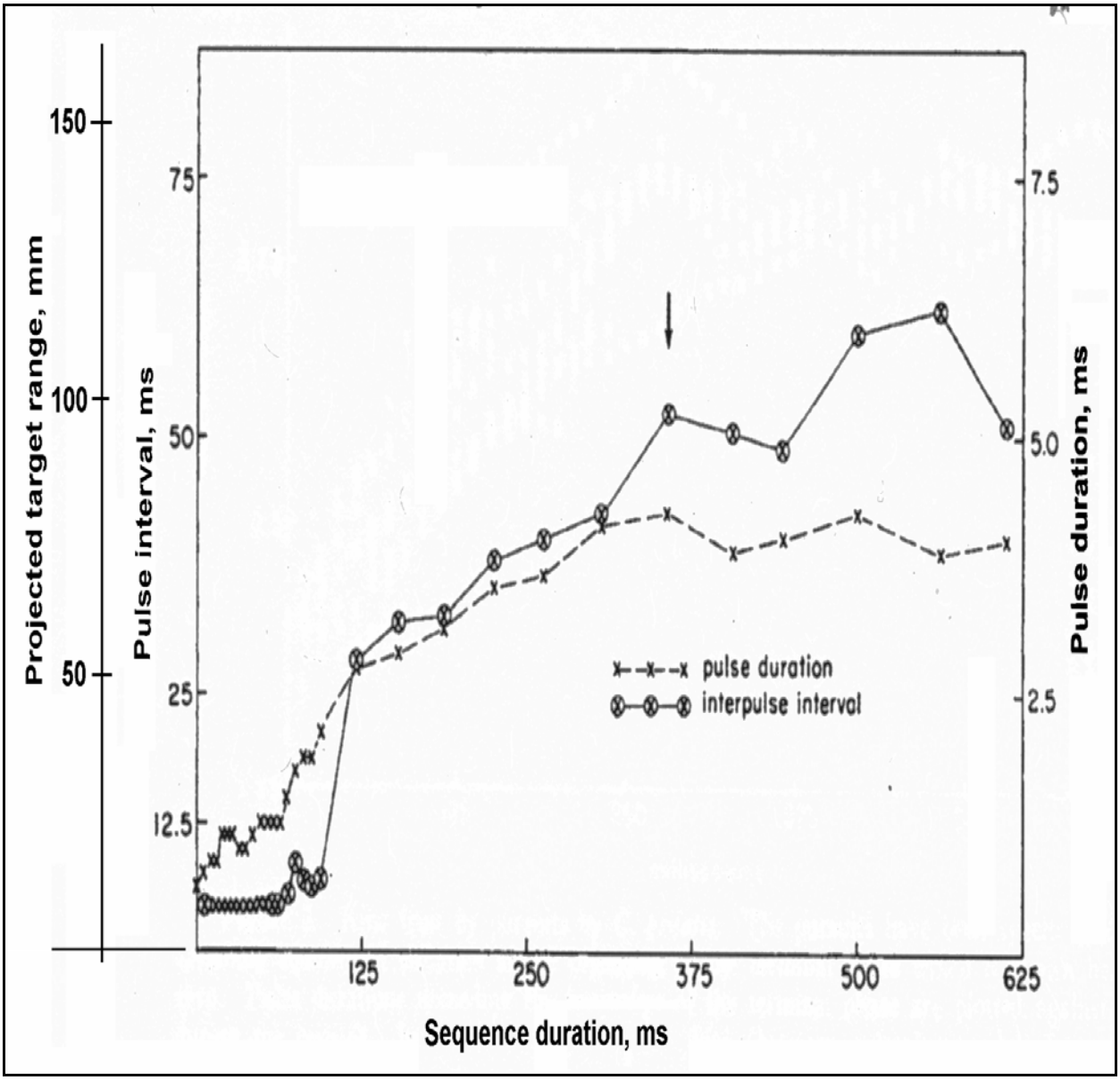


**Figure 1.2.3-1** An example of a fruit fly pursuit by *C. Psilotis*. Pulse duration and interpulse interval are plotted against time before the end of the pursuit. Assumed bat movement 1 ms = 1.73 mm. The projected target range is calculated from this value. The arrow indicates the first calculated pulse-echo overlap. Note; time reads from right to left (larger numbers represent earlier events). From Novick, 1965.

Roverud & Grinnell have provided a pair of papers discussing the detection and ranging capabilities

of the bat, *Noctilio albiventris*[108,109]. This bat is a member of the order *Microchiropteran*. Simmons et al. have provided a paper containing much data on a bat of the order *Chiropteran*[110]. However, their analyses are based on the use of techniques adopted from conventional man-made acoustic ranging equipment. As noted in the introduction to this appendix, bats (along with other mammals) are not capable of computing autocorrelation functions using transcendental calculations.

Using the gated time window technique described by Roverud & Grinnell instead of the differential time measurements of Simmons et al. leads to a physiologically feasible echolocation system.

Pollack has discussed the capabilities of the mustache bat, in considerable detail[111]. See also Appendix K of this work. His references to resonance in the cochlea are not explored in detail and are not supported by this work. However, his discussion of Doppler shift compensation to center the Doppler return from an insect ±10 Hz around 62.87 kHz is right on target. It is much easier to change the frequency of the active voice emission of the animal than to change the "tuning" of the sensitivity peak within the cochlea and the mapping of this sensitivity peak into the hypertrophied inferior colliculus.

Jakobsen, Ratcliffe & Surlykke have recently provided some valuable scaling information relative to the frequency of peak power output versus bat size and field of acoustic view[112].

## 1.3 The overall neural physiology of echolocation in dolphins

The transmitting and receiving functions associated with the dolphin offer a very wide range of potential signaling capabilities. It is important to consider these potentials in order to understand the operation of the neural system.

It has been shown (Fulton, 2004, 2005 & 2006) that the neural system is not capable of performing transcendental mathematical calculations (except for a natural logarithmic conversion) and contains no resonant circuits. The neural system is entirely temporal-based. The neural system is not capable of performing calculation involving sines and cosines and it is not able to perform Fourier transformations in the frequency domain.

It has also been shown that the neural system is place (as opposed to frequency) oriented. In both vision and hearing, the signals generated at specific locations within the retina and cochlea are processed by the remainder of the neural system. In this sense the systems are either retinotopic or

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[108]Roverud, R. & Grinnell, A. (1985) Discrimination performance and echolocation sighal integration requirements for traget detection and distance determination in the CF/FM bat, *Noctilio albiventris*. *J Com Physiol A* vol 156, pp 447-456

[109]Roverud, R. & Grinnell, A. (1985) Echolocation sound features processed to provide distance information in the CF/FM bat, *Noctilio albiventris*. *J Com Physiol A* vol 156, pp 457-469

[110]Simmons, J. Ferragamo, M. Moss, C. et al. (1990) Discrimination of jittered sonar echoes by the echolocating bat, *Eptesicus fuscus*: The shape of target images in echolocation *J Comp Physiol A* vol 167, pp 589-616

[111]Pollak, G. (1990) Adaptation of the mustache bat In Webster, D. Fay, R. & Popper, A. eds. The Evolutionary Biology of Hearing. NY: Springer Chapter 36

[112]Jakobsen, L. Ratcliffe, J. & Surlykke, A. (2013) Convergent acoustic field of view in echolocating bats *Nature* vol 493 pp 93-96

cochleotopic rather than directly related to the parameters of the environment ( such as tonotopic). This is important because, merely changing the curvature of the cochlea can change the frequency range to which the auditory system is sensitive without making any changes in the remainder of the neural system.

It should be appreciated that most of the following material in this section is based on inferences, based largely on comparative anatomy, that require future laboratory demonstration.

The neural system operates as a "pipeline" signal processor. Once data has been acquired at the cochlea, the signals are passed along multiple parallel channels within the system. There is no requirement that the processing within these channels be completed before the next data acquisition cycle begins.

It appears that most bottlenose dolphins do not emit a new acoustic signal until 19 to 30 ms after the reflection associated with the previous emission has been received at the outer ear. This is not true in the case of a beluga whale, *Delphinaterus leucas*, as shown by Turl & Penner, 1989. **Figure 1.3.1-1**, from Turl & Penner, shows one of the echolocation signal patterns used by a beluga whale when investigating a target at a range of 100 meters. The pattern shows the beluga sends out a series of closely spaced pulses and then pauses. This pause allows the last pulse to reach the target and return before any other pulse is emitted. This method of operation allows the beluga to determine the unambiguous range to the target, using the last pulse in each group, while achieving a higher signal to noise ratio with respect to the target by using multiple pulses where the target range could be interpreted ambiguously. This method should work best in open ocean situations where reverberation is not of major concern. The beluga employs two other pulse patterns that may be more useful in high background situations. Note the pulse spacing in the lower frame. The interval between pulses is near the fusion interval of the human visual system. It is likely that pulses are sent at intervals of near 30 ms to insure a perception of continuity between the individual perceived acoustic "images."

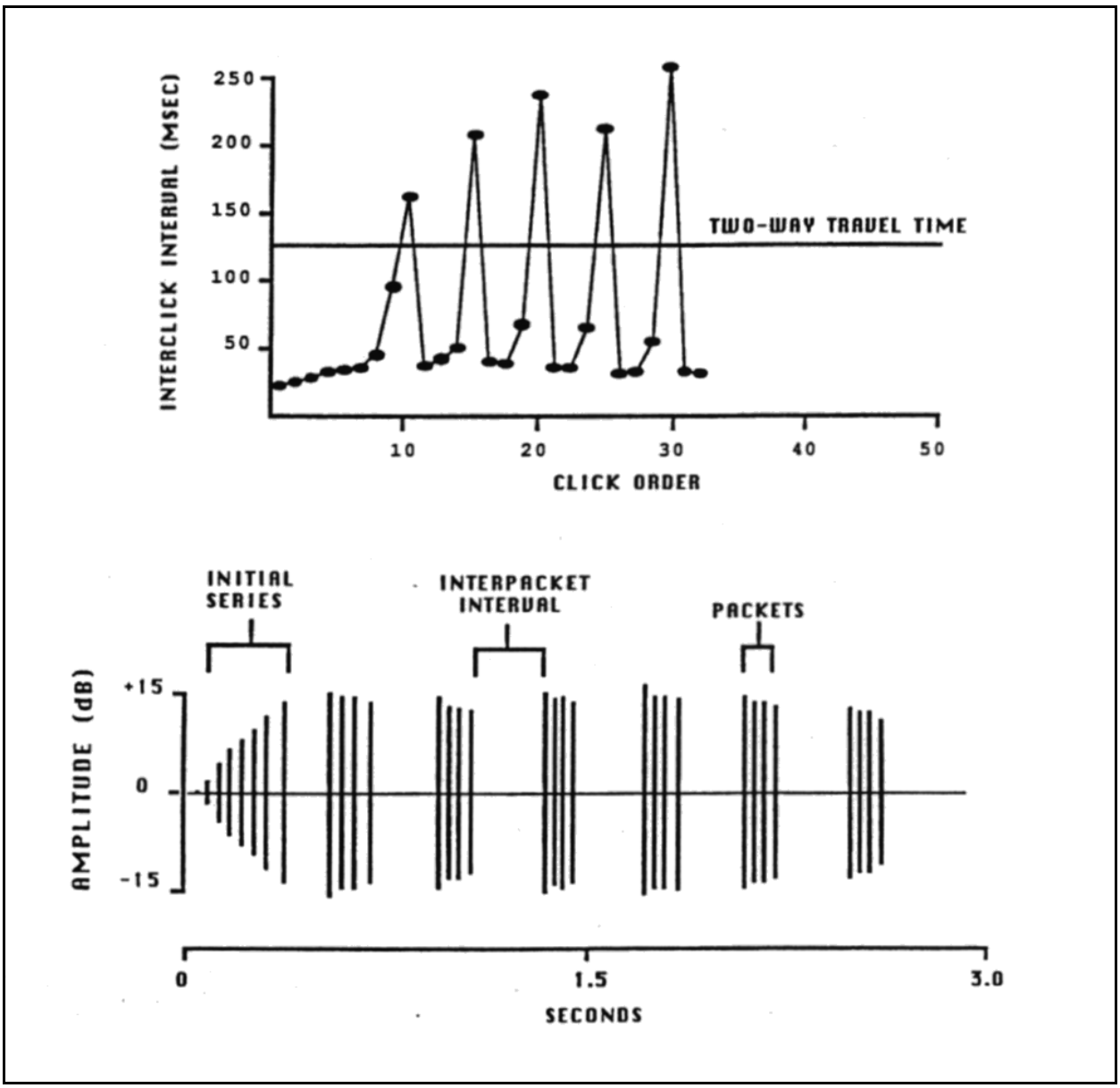


**Figure 1.3.1-1** A beluga whale click interval pattern for a target at 100 meters. Top; click interval versus click interval number. Bottom; amplitude versus time profile. From Turl & Penner, 1989.

## 1.3.1 Intrinsic signal generating capability of the dolphin

The transmitting and receiving functions associated with the dolphin offer a very wide range of potential signaling capabilities. It is important to consider these potentials in order to understand the operation of the neural system.

The signals that can be generated by the phonation system include those of both the larynx and the two mechanisms associated with the spiracular cavity. The basic forms of these signals include:
1. A complex broad band low frequency (LF) signal, 200 Hz to 15,000 kHz, not unlike that generated by other mammals of its size.

2. A swept narrow band signal operating within the HF range of 4,000 to 30,000 Hz.

3. A band limited impulse type signal occurring in the UHF range of 30 kHz to 150 kHz.

The literature is clear that at least two and probably three sources of acoustic energy can operate simultaneously in the dolphin. There is no question that at least two impulse type signals can be generated simultaneously as well as sequentially.

The complexity of the emitted signals makes their analysis, even their display prior to analysis by humans, awkward as well as difficult. The dynamic range of the emitted patterns as a function of time is difficult to capture in a display that also captures the long term signal characteristics. **Figure 1.3.1-2** is a poor copy of a waterfall display that illustrates the problem[113]. Only energies above 205 dB were displayed in this presentation and the animal was not allowed to approach the target. Moore & Pawloski also reported on their ability to train the dolphin to modulate its peak power output according to a pattern if not on command.

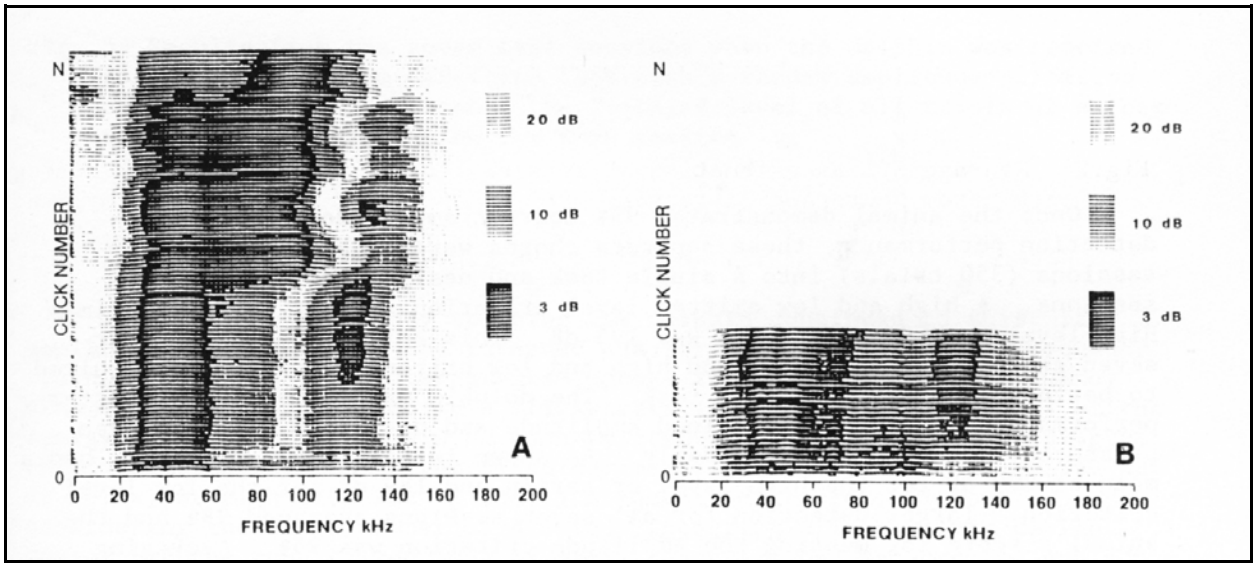


**Figure 1.3.1-2** Waterfall displays of the energy distribution in emitted clicks with a 205 dB threshold. An alternate display would present time on the horizontal axis. A similar display can present time on the vertical axis instead of click number. Each click is plotted vertically as a series of horizontal spectra. Three shades of gray represent the 20, 10, and 3 dB energy bandwidths. A; a click train of 101 clicks emitted during a search with no intentional target present. B; 29 clicks emitted during a target present trial. The animal left the station to report target acquisition. From Moore & Pawloski, 1989.

Frame A shows an initial few pulses that are unimodal. The sequence changes to a bimodal structure around click 5-10. This pattern is maintained until about pulse 85 when it returns to a monomodal form.

## 1.3.2 Potential signals received by the dolphin from its environment

The dolphin is exposed to and can be expected to process both passive signals generated by its environment and active signals generated by itself. The signals generated by the environment

[113]Moore, P. & Pawloski, D. (1989) Investigations on the control of echolocation pulses in the dolphin, *Tursiops truncatus In* Thomas, J. & Kastelein, R. Op. Cit pp 305-316

include potential communications signals from other members of its species. Because of the social character of the dolphins, it can be expected that the echolocation signals generated by one dolphin will be received by other dolphins and must be rejected as extraneous for their purposes.

This section will develop the characteristics of the potential signals used in dolphin echolocation. It will be seen that both time difference measurement (based on pulse transmission techniques) and spectrographic measurement techniques (involving frequency comparison and correlation processing) offer considerable utility to the dolphin.

The ability of the bottlenose dolphin to vary the character of its emitted signals dynamically makes identifying the features in a given received signal difficult. The received signal can vary from pulse to pulse, and quite possibly within the echo pulse due to frequency and amplitude changes within the emitted pulse generating the response.

### 1.3.2.1 Character of exogenous signals

The exogenous signal environment could be of interest to the dolphin for a variety of reasons. The reception of passive signals using binaural receiving techniques (even in the presence of interference) is well known from the experience of humans. However, the detailed analysis of this area is beyond the scope of this study of echolocation.

### 1.3.2.2 Character of the reflected endogenous signals

An active signal reflected from targets within the environment can be analyzed using a variety of techniques involving both time delays and frequency shifts. These capabilities have been widely used in man-made equipment using fixed frequency and swept frequency continuous tone signals as well as single and multiple pulse signals. It is appropriate to consider if and how the dolphin could employ these same techniques.

While it is well known that a target can be tracked by its reflected Doppler signal generated in response to a continuous fixed frequency tone reflected from a “moving” target. It is less well known that a target can be tracked by the change in received frequency at a given time in response to the transmission of a swept continuous tone signal.

It is also well known that a target can be tracked using the energy reflected by the target in response to interrogation by a pulse signal of known timing. Man has developed a wide range of display techniques allowing the extracted information concerning the targets to be presented to the senses of the human equipment operator.

All of the signals described above are processed more effectively using binaural receiving techniques.

#### 1.3.2.2.1 The reflective characteristics of fish

Textbooks frequently describe the reflection of acoustic energy from fish in analogy with the reflection from the skin of aircraft in radar applications. Reference is also frequently made to the reflections from the moving appendages of fish. In general fish (including their appendages) have densities very similar to that of water. As a result the reflected signal, due to the impedance change at the surface of the fish, is quite small compared to that of an airplane. The situation is analogous to the modern stealth aircraft that employs composite materials to avoid radar reflections. While such a reflection can be detected, there is a more important reflector involved. The so-called swim-bladder, an internal bladder filled with air, represents a major impedance discontinuity between the

density of the fish and the air. As in the case of air sacs within the head of the dolphin, this swim-bladder acts as a very effective reflector of acoustic energy. The bladder plays a role analogous to the active transponder used in modern aircraft operations.

### 1.3.2.2.2 The character of reflected continuous tones

The detection of targets illuminated by continuous tones involves the sensing of differences in frequency between the radiated and received signals. These differences can involve a simple time delay due to the distance to the target or a shift in frequency due to a difference in relative velocity between the source and the target. Both of these changes are readily detected by a system with adequate means of remembering the characteristics of the transmitted signal at a given time. **Figure 1.3.2-1** caricatures some of the features of the signals involved in this mode of operation.

Frame A of the figure illustrates a simple continuous tone sonar (top line) and potential reflections from three targets. Target T1 is a fixed target. The frequency of the reflected signal is the same as the transmitted signal. The distance to the target can only be ascertained roughly as a multiple of the phase difference between the radiated and reflected signals (if within the bandwidth of the receiving circuitry). Target T2 is closer to the emitter and moving toward it as shown by the larger amplitude and higher frequency of the received signal. Target T3 is moving away from the emitter as shown by the lower frequency of the received signal. This system has low utility because of the ambiguity in the range estimation.

Frame B shows a more utilitarian swept continuous tone system. The source is shown as a dashed line. A nearby target generates a reflection as shown by the left solid line. Such a reflection might indicate a nearby surface. The right portion of the figure shows a more interesting situation. The reflected signal complex consists of a continuous swept tone representing a simple target at a longer range. Associated with this signal are additional signal components associated with elements of the complex. These signals can be associated with other elements appearing and disappearing in the vicinity of the major target or as elements of the major target moving toward the emitter at different times and elements moving away from the emitter at different times. This could be a representation of a school of fish swirling about a common average range. In that case, the reflected pattern from the overall complex at a given time might resemble an ellipse as shown by the dotted line. It will be seen that this pattern is not significantly different from those associated with a chord of music, a set of tones occurring at a given time. Such musical patterns are readily identified by humans.

A swept continuous tone system is capable of good range resolution. Using the data of Caldwell (1990), the sweep rate for the bottlenose dolphin is on the order of 180-250 kHz/second. By storing a neural rendition of the emitted signal and comparing it with a received reflection, an estimate of the range of a target can be made. Such an estimate can be made simultaneously for every target within the range of the system using correlation techniques.

Simple envelope detection does not provide significant range information in a continuous amplitude tonal system, whether using a fixed or swept tone. However, the dolphin uses a frequency dispersion system to detect tonal energy within each of many narrow bands to which it is sensitive. Envelope detection of this energy can be used for ranging as well. The differential associated with the leading edge of these reflected envelopes can be compared with the reference sample with considerable accuracy. A value of 50 microseconds is frequently found in human psychophysical and animal electro-physiological tests. If achieved in the tonal channels of the dolphin, this accuracy would suggest a range accuracy on the order of five to ten centimeters for the swept tonal system.

Frame C will be discussed in the next section.

The swept continuous tone biosonar, with the tone lasting up to a few seconds, appears admirably suited to the needs of the dolphin. It provides a large amount of information concerning a target complex in a form similar to that known to be used effectively by other animal auditory systems. It also allows the separation of multiple targets and backgrounds based on concepts similar to those known to be used by humans to separate a desired complex communications signal in the presence of interference.

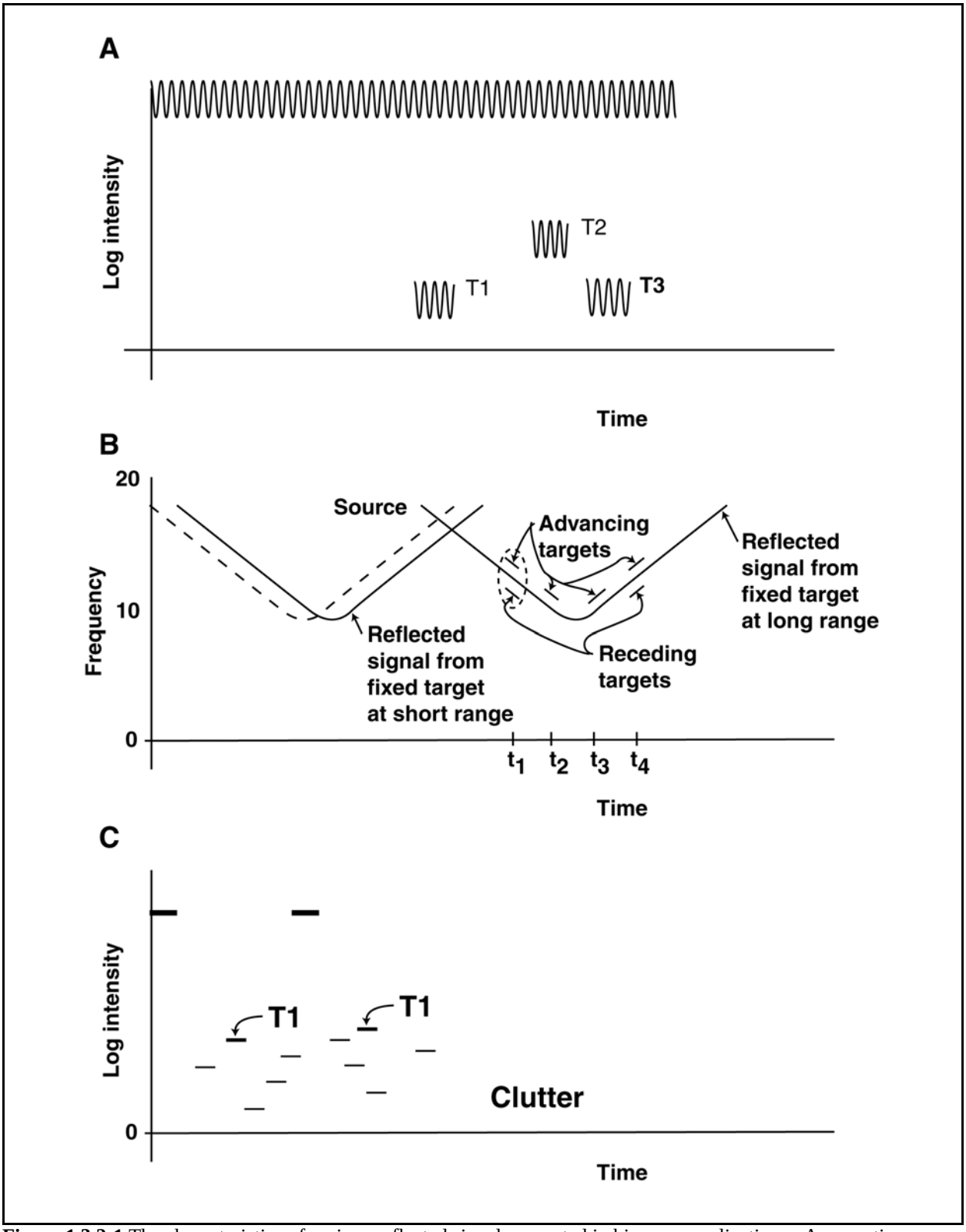


**Figure 1.3.2-1** The characteristics of various reflected signals expected in biosonar applications. A; a continuous fixed frequency signal and its reflection from three targets. B; a continuous swept frequency signal and several reflections. C; a pulse signal reflected from a target and clutter due to the background. See text.

### 1.3.2.2.3 The character of reflected impulse signals

The basic monaural and binaural processing of reflected pulse information by animals is based on the time of arrival of the reflected signal without regard to the phase of the high frequency content of the pulse or of the relative phase between the high frequency content of the signals received at the two ears. There is an exception to this for signals at frequencies below 600 Hz (and possibly below 1,000 Hz). The early circuits of the auditory system are capable of reporting amplitude variations (and therefore phase relationships) at frequencies below this limit. As a result, the binaural capability in humans can be shown to use both the time of arrival and the phase difference information (for low frequencies) in its determination of source angular location. It would be expected that the same capability would be available to dolphins.

Frame C of the above figure illustrates the monaural signals involved in an impulse-based echolocation system. Following an initial high intensity pulse from the emitter, a complex of reflected signals is typically received. These signals typically consist of a signal from an unidentified target plus signals from the local surface and bottom of the sea (generally described as reverberations) and signals from other extraneous objects in the background. The background and reverberations are frequently described as clutter. The problem of target isolation is frequently solved by emitting multiple impulses and performing frame-to-frame subtraction on the received signals to isolate moving targets. Once a target (moving within an appropriate velocity with respect to the emitter) has been isolated, simple windowing techniques, similar to those used in man-made systems, can be employed to suppress the clutter and emphasize the return from the target.

While it is possible to extract both position and velocity information from signals generated by the reflection of continuous trains of impulse, the process is difficult and incompatible with the basic architecture of biosonar. Impulse-based biosonars appear designed specifically to exploit single pulse mapping techniques.

### 1.3.2.2.4 Useful biosonar configurations

Based on the above discussion, it appears obvious that the dolphin would be well served by either a swept continuous tone type of sonar or a simple monopulse type of sonar. If it was able to combine these two types, additional advantages would probably be obtained that are not obtainable from only one type. Based on the combination of whistle and click signals emitted by most dolphins, it appears this dual capability has been achieved.

Caldwell, et. al. have noted in Leatherwood & Reeves that infant dolphins do not exhibit a signature whistle (an orderly swept continuous tone signal). However, they develop a signature whistle well within their first year. This development would be compatible with the process of appreciating the utility of the responses to such signals and memorizing (learning) the patterns received as they relate to food sources.

## 1.3.3 Extensions based on binaural and biphonic implementations

The mammalian echolocation system employs two techniques not found in typical man-made radar and sonar systems, the use of two separated receiving apertures (as in most lateral animals) and two independent transmitting sources forming a beam through a common projection system.

Humans are known to use binaural hearing for passive source location and signal discrimination. Both phase differences and time of arrival differences are used. It must be assumed that the dolphins share this capability.

The use of two transmitting sources simultaneously could generate controllable interference patterns in the far field pattern of the transmitting system that would significantly change the short term reflected energy received as a function of distance from the sources. Such a system could provide additional information about the longitudinal dimensions of any targets. Signals generated by the dual beams of a dolphin have been reported, but based on only unsophisticated instrumentation.

### 1.3.4 The potential neural architecture of the dolphin

The overall target location capability of the dolphin can be estimated initially by comparing its morphology with that of other mammals, particularly the human (extensively analyzed behaviorally), the cat (extensively analyzed physiologically) and the bats (extensively analyzed both behaviorally and physiologically).

It is likely that the capabilities of the dolphin to analyze the non-location aspects of signals from its passive environment are similar to that of other mammals. Such perception is focused in the diencephalon (perigeniculate nucleus and pulvinar of the thalamus) and in the temporal lobe of the cerebral cortex.

The ability of the human and other mammals to locate sources is well quantified. This ability has been traced to the binaural capability of the generic auditory system residing largely in the inferior colliculus. This capability has been found to consist of two separate sub-capabilities. One sub-capability, extending up to about 600 Hz in humans, employs phase sensitive binaural signal processing in the tonal signaling portion of the system. The second sub-capability relies upon relative time delays measured by the binaural component of the temporal signaling system. It is likely that the dolphin is able to utilize these same passive capabilities.

The ability of a system employing an impulse type illumination source could operate much like the above passive sub-capability based on the temporal portion of the binaural system. Such a capability is likely to be found associated with the inferior colliculus or its homologs.

The ability of a system employing an active swept continuous tone source could operate much like the above passive sub-capability based on the tonal portion of the binaural system. This is a capability not found in mammals other than possibly in the bats. It would be expected to require significant neural signal manipulation capability. The logical source of this capability would be the lateral lemniscus, an engine largely without known purpose and nearly vestigial in humans and many other mammals. The lateral lemniscus are large and highly elaborated in the dolphin.

It is proposed the information acquisition portion of the hearing system of the dolphin;
- is highly developed for both communications and target location,
- is capable of target location using both passive and active techniques,
- uses both swept continuous tone and impulse forms of biosonar for echolocation, and
- employs both binaural and biphonic techniques beyond the scope of most man-made sonars.

It is proposed the neural signal generation portion of the hearing system;
- is typical of that used in other mammals,
- is uniquely shielded by reflective air sacs from the high intensity acoustic generation function,
- employs dispersion (rather than resonance) techniques for signal separation within the cochlea.

It is further proposed the information extraction portion of the hearing system of the dolphin can be described as consisting of three parts,
▸The first part is focused on intraspecies communications with activity centered in the thalamus of the diencephalon and the temporal lobes of the cortex (in common with other mammals).
▸The second part is focused on passive source location and precision pointing operations with activity centered in the inferior colliculus (in common with other mammals) and other elements of the PES (shared only with the bats).
▸The third part is focused on (acoustic) target imaging and analysis (using techniques homologous with those used in communications analysis) with activity centered in the lateral lemniscus of the brain.

Such a biosonar system significantly exceeds the capability of current man-made systems.

## 1.4 The neural physiology of specific circuits used for echolocation in dolphins

The block diagram of dolphin echolocation and the generic schematic of mammalian hearing described in **Section 1.1.2** can be expanded into detailed discussions of the individual engines of the dolphin neural system. To do this requires some background in the electrical operation of the basic neuron. It also requires recognition of the basic architecture of neural signaling. Finally, putting matters in perspective is easier if it is noted that each neural center dedicated to a specific task consists of more than four million individual neural circuits. Because of the overall complexity of these individual centers, they are defined as engines in this work. This name correlates very well with the engines defined in current computer processing. An engine is a major hardware portion of a computer that incorporates memory as well as algebraic manipulation and frequently employs its own specialized software routines.

Neurons can be divided into three basic groups, the sensory neurons, the signal processing neurons, and the signal projection neurons. The sensory and signal processing neurons operate in the analog mode. Only the signal projection neurons operate in the phasic mode (and generate action potentials).

Within the cortex, projection neurons are used to interconnect the different feature extraction engines and logic units of the brain with the initial motor system command generation centers. Projection neurons typically connect remote neural engines (separations larger than two millimeters).

These concepts are explored in greater detail in Chapter 8 of "Processes in Biological Vision[114]."

### 1.4.1 Overview of the electrolytic neuron

The electrolytic theory of the neuron presented in "Processes in Biological Hearing," (the parent of this paper) has provided an entirely different context for neural operation than the previous chemistry-based hypothesis. The electrolytic context allows description of the operation of the neural system at a level never addressed under the chemical hypothesis.

#### 1.4.1.1 Basic physiological forms of neurons

The fundamental neuron is a three-terminal electrical device. The principal terminals of the device are the dendritic terminal, the poditic (base or foot) terminal and the axon terminal. Together, the

[114]Fulton, J. (2005) Processes in Biological Vision. www.sightresearch.net

dendritic and poditic terminals are called neurites. In the morphology of a typical neuron with two neurite arborizations, one is dendritic and the other is poditic. The neuron forms a circuit similar to a conventional transistor circuit and contains at least one equivalent semiconductor device called an Activa. The most common circuit form used in the neural system employs the Activa in a grounded base (podite) circuit. A synapse is also a circuit containing an Activa connected to form an electrical diode. These configurations and their performance are discussed in detail in www.hearingresearch.net/pdf/4Physiology1.pdf Only the outer and inner hair cells use a more complicated circuit. The circuit of these cells is discussed in www.hearingresearch.net/pdf/5Generation.pdf

### 1.4.1.2 The bandwidth and propagation velocity of myelinated neurons

The literature contains a variety of comments concerning the propagation velocity of neural signals. Little justification is given for these comments except for a general expression that velocity is a function of the diameter of the axon.

It is very important to distinguish between the actual diameter of the axon of a myelinated neuron and the overall diameter of the axon/myelination combination. The actual diameter of most neurons varies very little. However, the thickness of the myelination can be so great as to vary the diameter of the combination by a factor of ten. It is the reduction in the capacitance per unit length of the axon due to the thickness of the myelination that determines the propagation velocity of the axon. This subject is addressed in detail at www.4colorvision.com/neuron/pdf/6Electrophysiol.pdf

The morphology of a signal propagation neuron, includes a series of Nodes of Ranvier along the length of its axon. Each Node of Ranvier acts as a regenerative repeater of the signal traveling along the axon. The repeater introduces a significant time delay. As a result, the average propagation velocity of a signal projection neuron is dominated by the sum of the repeater delays. As a result, the nominal (first order) neural projection velocity over lengths longer than two millimeters is 44 meters/sec. This number is much smaller than the 4400 meters/sec achieved by the intrinsic axon segment between two regenerators.

The bandwidth of the axon is largely determined by the maximum clock speed of the action potentials generated by the projection neuron and its Nodes of Ranvier. For most projection neurons, this bandwidth is about 250-300 Hz. For some projection neurons between the spiral ganglia and the inferior colliculus, this bandwidth approaches 600 Hz in many mammals. There are indications that similar circuits in the dolphin may achieve 900-1000 Hz. This would be an adaptation to optimize the primary echolocation servo (PES) loop and provide the best possible biosonar range resolution in the impulse part of the system.

## 1.4.2 The acoustic receiving & signal generation system in dolphins

### 1.4.2.1 Technical background & definitions

Dolphin hearing researchers have developed a term of art that is poorly defined in the literature. They compare dolphin hearing with an “energy detector.” In electrical engineering, a detector comes in a variety of forms. Some forms are envelope sensitive, some forms are phase sensitive and some forms are frequency sensitive. In photosensitive systems, the detector is either thermal energy sensitive or photon flux sensitive. Thermal energy detectors are usually thought of as sensitive to a

broad frequency range of radiant energy without regard to the phase of the individual frequency components of that energy. Energy detectors typically have very long time constants and do not respond to changes rapidly. This includes changes in the envelope of the applied signal. From the context, it appears dolphin researchers imply this form of energy detector. However, there are clear examples where this is not the type of detector used by the dolphin. The phase sensitivity of the dolphin signal detectors will be discussed below.

Dispersion is a term of art that has not appeared previously in dolphin research related to the cochlea. Acoustic dispersion is the spreading of energy associated with an initial signal in either the temporal or frequency domain. Temporal dispersion of a longitudinal acoustic wave is found theoretically in both Newtonian and non-Newtonian fluids. The result is different velocities for frequency components as a function of their frequency. Both fresh and salt water at temperatures significantly above their freezing point are Newtonian fluids but they show negligible dispersion in the context of hearing. This is not true of silt laden water. Silt laden water is highly non-Newtonian, exhibits measurable temporal dispersion, but is of little interest here.

Frequency dispersion of acoustic energy may occur in analogy with light passing through a prism. In the cochlea, the energy associated with an initial signal travels as a surface acoustic wave along Hensen's stripe on the surface of the tectorial membrane. As the curvature of Hensen's stripe varies, the energy is dispersed spatially across the surface of the tectorial membrane.

### 1.4.2.2 Details of acoustic energy reception in the dolphin

Acoustic antenna rules would suggest the outer ears of dolphins perform in two different modes depending on the frequency of operation. At low frequency, the wavelengths of signals in water are longer than the individual elements of the receiving system. This suggests that at low frequencies, dolphin hearing is largely omnidirectional. It also suggests, the outer ear is merely an impedance matching device between the water and the entrance to the cochlea of the inner ear. At frequencies above 15-30 kHz, the wavelengths of sound are much shorter. In this higher range, the receiving (and transmitting) elements of the dolphin support highly directional antennas.

The literature does not provide a detailed description of the outer ear of the dolphin when operating at high frequency. It only notes the outer ear is based on a graded index form of dielectric antenna, instead of the horn type of antenna used by other mammals. The dielectric form allows a hydrodynamic exterior surface that is compatible with a forward looking receiving system yet meets the requirements of high speed swimming. The problem in defining the dolphin antenna is twofold. Insufficient detail is available concerning the fatty tissue material along the lower posterior jaw of the dolphin and it is quite likely, the precise geometric form of the fatty material is under the muscular control of the dolphin. While the figure in **Section 1.1.3** shows the dolphin outer ears as viewed from the front, many other pictures and drawings suggest significantly different external appearances for the outer ears (See Reynolds, 2000).

#### 1.4.2.2.1 A physiologically compatible lens antenna for reception

A simple description of the external ear of the bottlenose dolphin is shown in **Figure 1.4.2-1**based on the lower half of the head of the dolphin in [**Figure 1.2.2-2** ] from Norris. The fatty tissue deposits appear to form a lens-type antenna between the vestibule of the labyrinth and the exterior water environment. The fatty deposits are known to vary in density. Hence, the lens-type antenna is of the variable density gradient type. A variable density contributes to a shorter antenna for a given degree of quality (minimizing sidelobes in the far-field pattern for a given aperture size).

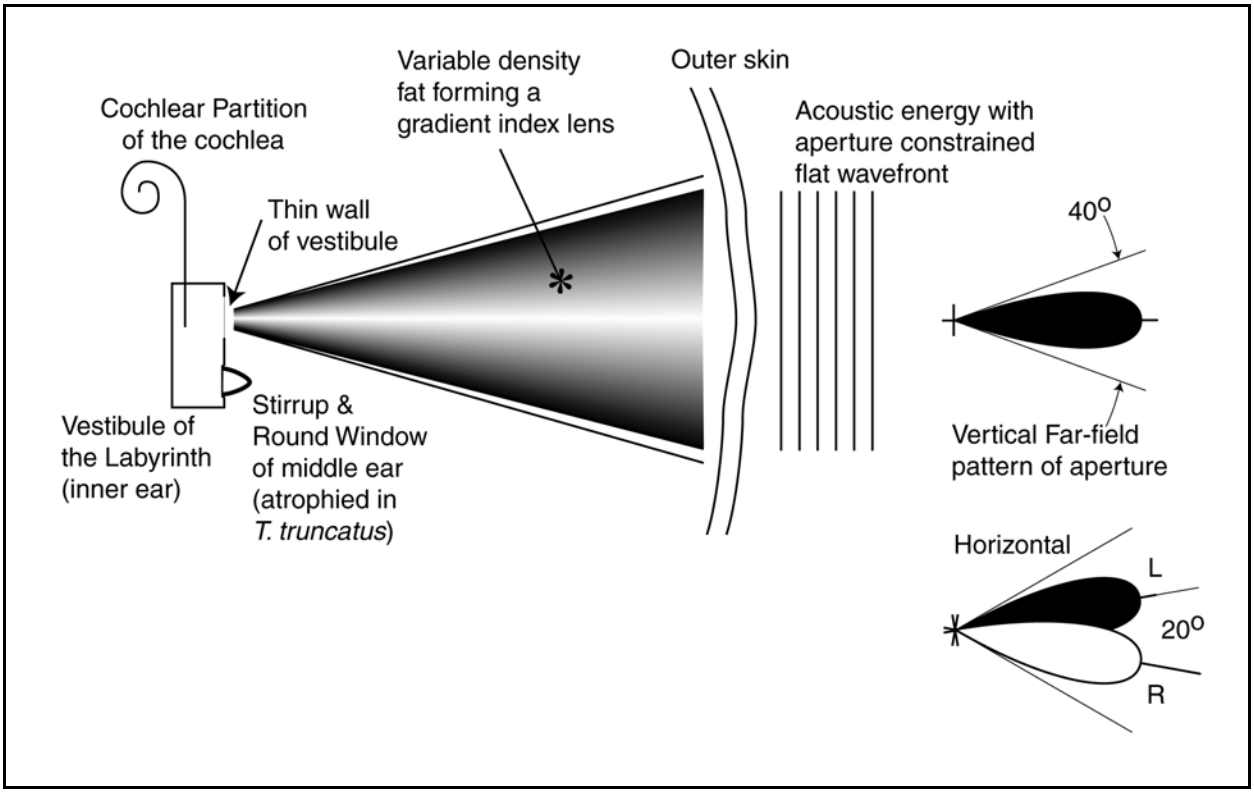


**Figure 1.4.2-1** The outer ear and field patterns of the bottlenose dolphin. The outer ear is a variable density acoustic lens formed of the fatty deposits at the rear of, and alongside, the lower jawbone. The outer ear acts like a Galilean telescope, transforming a low energy density planar wavefront at the aperture into a higher density wavefront of greater curvature at the entrance to the labyrinth and inner ear. The energy delivered to the labyrinth is transferred to the cochlear partition where it is processed conventionally. The beam pattern is nominally 20 degrees between nulls and is independent of acoustic frequency. The horizontal "squint angle" between left and right ears is shown at 20 degrees.

The goal of any lens-type receiving antenna is to deliver energy to the receiving circuitry at a higher power density than present at the aperture of the antenna. A lens-type antenna is not as frequency sensitive, within the limits of geometrical optics, as most types of antennas . The design offers minimum sidelobe sensitivity, as observed in practice. The angular size of the main lobe is based on the aperture of the antenna and the wavelength of the energy involved.

The delivery of the acoustic energy to a thin section of the vestibule of the labyrinth explains one of the unknowns in earlier dolphin research, how the auditory system worked with the obviously atrophied and disconnected bones of the middle ear. As noted earlier, an aquatic animal has no need for the impedance conversion function provided by these bones in the terrestrial middle ear.

The "squint angle"between the two ears , a term adopted from radar design, is shown as 20 degrees in the horizontal plane. This is the value used by Au & Moore as nominal. A feature of the variable density lens-type external ear is the ability to change the squint angle easily under muscular control. Under optimum hydrodynamic drag conditions, the squint angle can be larger and provide a broader search capability of low resolution. The squint angle can be reduced during an attack phase to achieve greater angular precision in target tracking and identification but at some loss in hydrodynamic efficiency.

### 1.4.2.2.2 The potential for the teeth to form an antenna in dolphins

Goodson & Klinowska proposed in 1989 that the equally spaced teeth of the bottlenose dolphin *T. truncatus* might form an antenna array providing a narrow forward-pointing beam supporting the hearing modality[115]. The proposal was primarily conceptual. It was based on certain anatomical observations concerning the teeth and offered no details of the relevant physiology of the dolphin. No comprehensive discussion of potential antenna designs was presented. Dobbins recently presented a design review of the Goodson & Klinowska antenna proposal based on the academic studies of two of his students[116]. While providing a competent analysis of the performance of a beam forming array of elements, it did not discuss the relevance of such an array to the physiology or neurology of the dolphin (page 27). Neither did it address one of the most frequent criticisms of the approach, the ability of dolphins who have lost their teeth to achieve apparently normal echolocation performance. A second argument against the approach is that the hardness of the teeth is incompatible with the absorption of acoustic energy from the environment or the soft tissue of the jaw.

### 1.4.2.2.3 The potential for the mental foramens to form an antenna in dolphins

Ryabov has provided an analysis of dolphin hearing focused on the presence of certain structures adjacent to the lower mandible of the dolphin[117]. The paper suffers a variety of semantic problems, having been formulated in Ukrainian or Russian and translated into English.

> The paper describes a set of lipid tissue structures adjacent to the lower mandible and described as mental foramens. This differs from the conventional use of these terms in human (and presumably dolphin) anatomy. Conventionally, the mental foramen is one of two holes ("foramina") located on the anterior surface of the mandible. It permits passage of the mental nerve and vascular vessels to the exterior surface of the skin covering the mandible. It does not refer to an external opening in the skin. Nor does it refer to lipid masses between the mandible and the skin..

Ryabov discusses the set of structures he defines as mental foramens within the concept of a traveling wave antenna. However, he does not develop the concept of a traveling wave antenna into a discussion of the specific sizes and relative spacing of the elements so critical to the operation of a traveling wave antenna. Nor doe he develop any acoustic field patterns associated with his proposed antennas. Specifically, he does not develop the difference in field pattern generated by the assymetrical arrangement of his left and right arrays of mental foramens. It is difficult to describe an array of only three elements as a traveling wave antenna.

Ryabov does not provide any lipid density values for his mental foramens that would allow computation of their performance in an acoustic antenna array.

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[115]Goodson, A. & Klinowska, M. (1989) A proposed echolocation receptor for the bottlenose dolphin (*Tursiops truncatus*) *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans, Vol 196. NY: Plenum pp 255-267

[116]Dobbins, P. (2007) Dolphin sonar–modelling a new receiver concept *Bioinspiration & Biomimetics* vol 2, pp 19-29

[117]Ryabov, V. (2010) Role of the mental foramens in dolphin hearing *Natural Sci* vol 2(6), pp 646-653

While Ryabov's array of mental foramens could act as directors in front of the acoustic horns defined in this work. The measured field patterns of these horn antennas do not suggest the presence of any directors in the near field of the acoustic receiving system.

Ryabov did recognize the finding of Norris (1964) that the low frequency performance of the dolphin radiating system was significantly different from the high frequency performance. He did not localize the important elements of the auditory receiving system at low frequencies except to say it was in the area of the external auditory meatus. In this work, the auditory meatus is irrelevant since the omnidirectional sensitivity of the dolphin hearing at low frequency, is based on the nominally uniform acoustic density of the bulk of the dolphins head forward of the cranium (except for the nasal cavities generally dorsal to the cochlea of the inner ear). The higher density of the mandible and teeth are irrelevant since they are located outside the transmitting antenna and receiving antenna field patterns. They can be considered in the shadows of the overall acoustic system.

### 1.4.2.3 Details of the frequency selection mechanism in the dolphin

The energy acquired by the outer ear is delivered to the inner ear and the cochlea as in all mammals. The cochlea of the dolphin is remarkably similar to that of humans in size and internal organization. It operates under the same principles as the human cochlea. The variable curvature of the critical element of the mechanism, Hensen's stripe, causes the acoustic energy to be dispersed as a function of frequency without the use of any resonant circuit elements.

Wever, et. al. presented a series of four papers on the anatomy of the cochlea in 1971-72. The last in March 1972 (referenced below) provides references to the earlier papers. They showed the cross-section of the cochlea is very similar to that of other mammals, except the individual elements are much more rigid[118]. **Figure 1.4.2-2** described the curvature of the cochlea in this species compared to that of human[119]. Using the theory of this work, the dolphin shows much higher discrimination capability in the high frequency region because of the low change in curvature with rotation in the outer portion of the cochlear partition. While one might assume the shorter cochlear partition would lead to a more limited acoustic range than humans, this is misleading. It is the maximum and minimum ***rate of change in curvature*** that determines overall frequency range of a species. The change in curvature with rotation in the inner ear is less than in humans over much of its range. The human cochlear partition is known to exhibit an increased curvature near it's apical (small diameter) terminus that has been labeled a "hook." The dolphin cochlear partition also appears to exhibit such a hook.

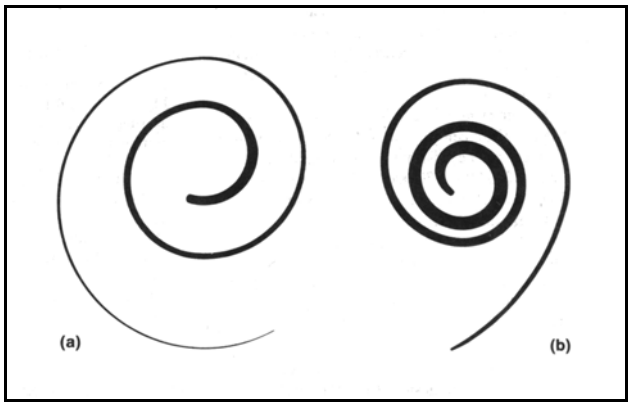


**Figure 1.4.2-2** A comparison of dolphin and human cochlear curvatures drawn to the same scale. The dolphin (a) shows much lower curvature per unit rotation in the high frequency outer region but a shorter cochlear partition and higher curvature per unit rotation in the low frequency region. From Wever et al., 1971.

[118]Wever, E. McCormick, J. Palin, J. & Ridgway, S. (1971) The cochlea of the dolphin, *Tursiops truncatus*: general morphology *Proc Nat Acad Sci USA* vol 68(10), pp 2381-2385

[119]Wever, E. McCormick, J. Palin, J. & Ridgway, S. (1971) The cochlea of the dolphin, *Tursiops truncatus*: the basilar membrane *Proc Nat Acad Sci USA* vol 68(11), pp 2708-2711

Wever et al. (1972, p.659) discuss the variations in the uniformity of curvature in a related dolphin species, the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*[120]. They note significant variations in the curvature among specimens which they relate to growth anomalies. While probably true, these anomalies would result in significant differences in local frequency discrimination capability in these specimens. These differences would probably not be recognizable in any but the most sophisticated evaluation programs. A variety of parameters in *L. obliquidens* and *T. truncatus* are compared by these authors.

Ketten & Wartzok have also studied the cochlea and provided dimensions of the cochlear partition[121]. They describe the shape of the cochlear partition of Delphinidae as a gnomonic (logarithmic) or equiangular spiral based on the "lateral edge" of the cochlear partition. While their data captures a variety of ratios related to the physical parameters of the cochlear partition, they do not adequately capture the geometry of the critically important tectorial membrane. It appears their lateral edge is the outer edge of the partition rather than the inner edge adjacent to Hensen's stripe. The use of the inner edge would introduce some differences in their data. They define a type I and type II spirals. The type II, equiangular (or logarithmic) spiral is only a first order approximation to the modified Hankel function actually used in the dolphins and other mammals. The modified Hankel function is discussed in a following section. Their type I Archimedean spiral appears to be a perturbation on the type I of this work.

Ketten provided a graphic of the cochlear spiral of *Delphinidia* in 1992[122]. **Figure 1.4.2-3** shows her figure. The change in the rate of change of curvature of the cochlear partition near the indicated mark allows the family to achieve higher frequency resolution in the higher frequency range without significant loss in resolution at lower frequencies.

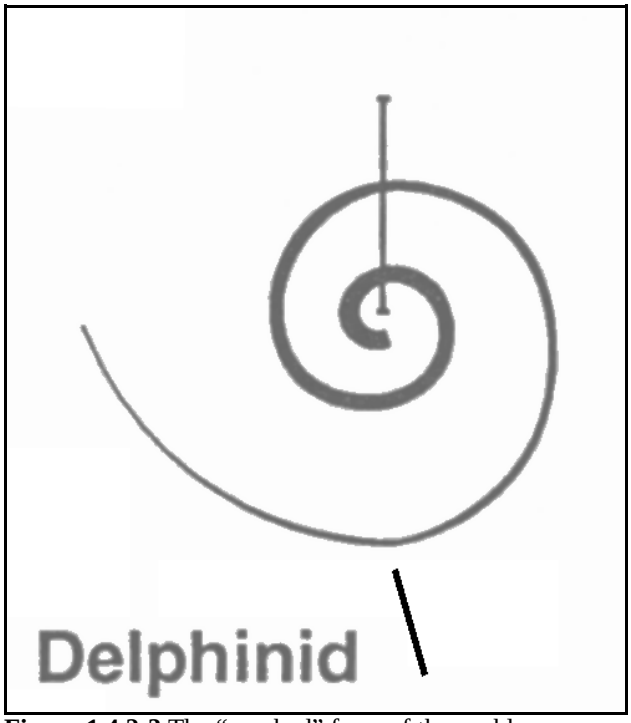


**Figure 1.4.2-3** The "cranked" form of the cochlear partition in *Delphinidia*. The change in the rate of change of curvature near the mark is difficult to see. The change accounts for the heightened frequency resolution of *Delphinidia* at high frequencies. From Ketten, 1992.

In the same paper, Ketten showed the cochlear spiral for a variety of Cetacea (page 68). Knowing that it is the rate of change of the curvature allows one to see how these different species are optimized to marginally different environments.

Two other important factors related to frequency discrimination have been reported.

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[120]Wever, E. McCormick, J. Palin, J. & Ridgway, S. (1972) Cochlear structure in the dolphin, *Lagenorhynchus obliquidens Proc Nat Acad Sci USA* vol 69(3), pp 657-661

[121]Ketten, D. & Wartzok, D. (1989) Three-dimensional reconstructions of the dolphin ear *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pp 81-105

[122]Ketten, D. (1992) The cetacean ear: form, frequency, and evolution *In* Thomas, J. Kastelein, R. & Supin, A. *eds*. Marine Mammal Sensory Systems. NY: Plenum pp 53+

As found in other mammals, the dolphin exhibits a critical bandwidth. This critical bandwidth can be considered the effective noise bandwidth of the animals receiving system. Alternately, it can be considered the bandwidth over which the animal is able to correlate frequency information as part of the information extraction process within the brain. The critical bandwidth of the dolphin appears to be similar to other mammals. Lemonds, et. al. have provided values for the critical band at several frequencies[123]. They report 16% of center frequency at 40 kHz to 11% of center frequency at 100 kHz.

The critical bandwidth figure, and the large size of the medial geniculate nuclei in the dolphin make it very likely that the dolphin employs the same spatial correlation mechanisms as employed by humans in both the visual and auditory domain. This would suggest the dolphin can in fact "image" targets examined by its active sonar system at a quality level yet to be determined. The limiting resolution of this imaging capability would be on the order of one-quarter wavelength or about 0.25 cm at 150 kHz. If correct, future exploration of the diencephalon of the dolphin brain should focus on describing the reticulated portion(s) of the very large (relative to human) medial geniculate nuclei. It may be possible to locate the portions described as the perigeniculate nuclei in this work (**Section 1.3.3**).

Wever, et. al. of 1971 (p. 2911) compare the number of hair cells and ganglion cells of the dolphin and human cochlea[124]. While the number of hair cells is remarkably similar to humans, the number of ganglion cells differs considerably. The bottlenose has about three times as many ganglion cells as the human.

Some of the axons in the auditory nerve of the dolphin are known to be quite large. Size in this area allows the transmission of wider bandwidth action potential pulse streams. A few terrestrial animals are known to project signals over the stage 3 signal projection circuits leading to the inferior colliculus at up to 600 Hz. It is quite possible that the dolphin can project signals over these circuits up to at least 1,000 Hz and possibly 3,000 Hz[125]. If this is confirmed by more detailed experiments, it would mean the dolphin could employ its two primary auditory channels as phase coherent receivers up to 1,000 Hz. Such operation would improve its horizontal spatial angular resolution considerably over that achievable by other mammals.

### 1.4.2.4 Details of neural signal generation in the dolphin

The generation of neural signals in the dolphin follows the general plan of mammals. The shape and length of the cochlea and the arrangement of the hair cells are remarkably similar to that of humans. Ketten has tabulated the parameters of the cochlear partition for a variety of animals[126]. The principal deviation between the bottlenose dolphin and the human is in the specific curvature of Hensen's stripe in the cochlea. This deviation accounts for the difference in frequency range and differential frequency sensitivity of the dolphin cochlea compared to other species.

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[123]Lemonds, D. Au, W. Nachtigall, P. Roitblat, H. & Vlachos, S. (2000) High frequency auditory filter shapes in an Atlantic bottlenose dolphin *J Acoust Soc Am* vol 108(5), Pt 2, pg 2614

[124]Wever, E. McCormick, J. Palin, J. & Ridgway, S. (1971) The cochlea of the dolphin, *Tursiops truncatus*: hair cells and ganglion cells *Proc Nat Acad Sci USA* vol 68(12), pp 2908-2912

[125]Zook, J. & DiCaprio, R. (1989) A potential system of delay-lines in the dolphin auditory brainstem *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pg 190

[126]Ketten, D. (2000) Cetacean ears *In* Au, W. Popper, A. & Fay, R. *eds*. Hearing by Whales and Dolphins. NY: Springer Chapter 2

The morphology of the cochlea of the dolphin is virtually indistinguishable from that of the human. Therefore, available caricatures from the human in Chapter 4 of "Processes in Biological Hearing" can be used here effectively. **Figure 1.4.2-4** shows the typical method of signal generation in mammals. Cartoons describing this mechanism are available at http://hearingresearch.net/anim/extraction.htm and http://hearingresearch.net/anim/separation.htm .

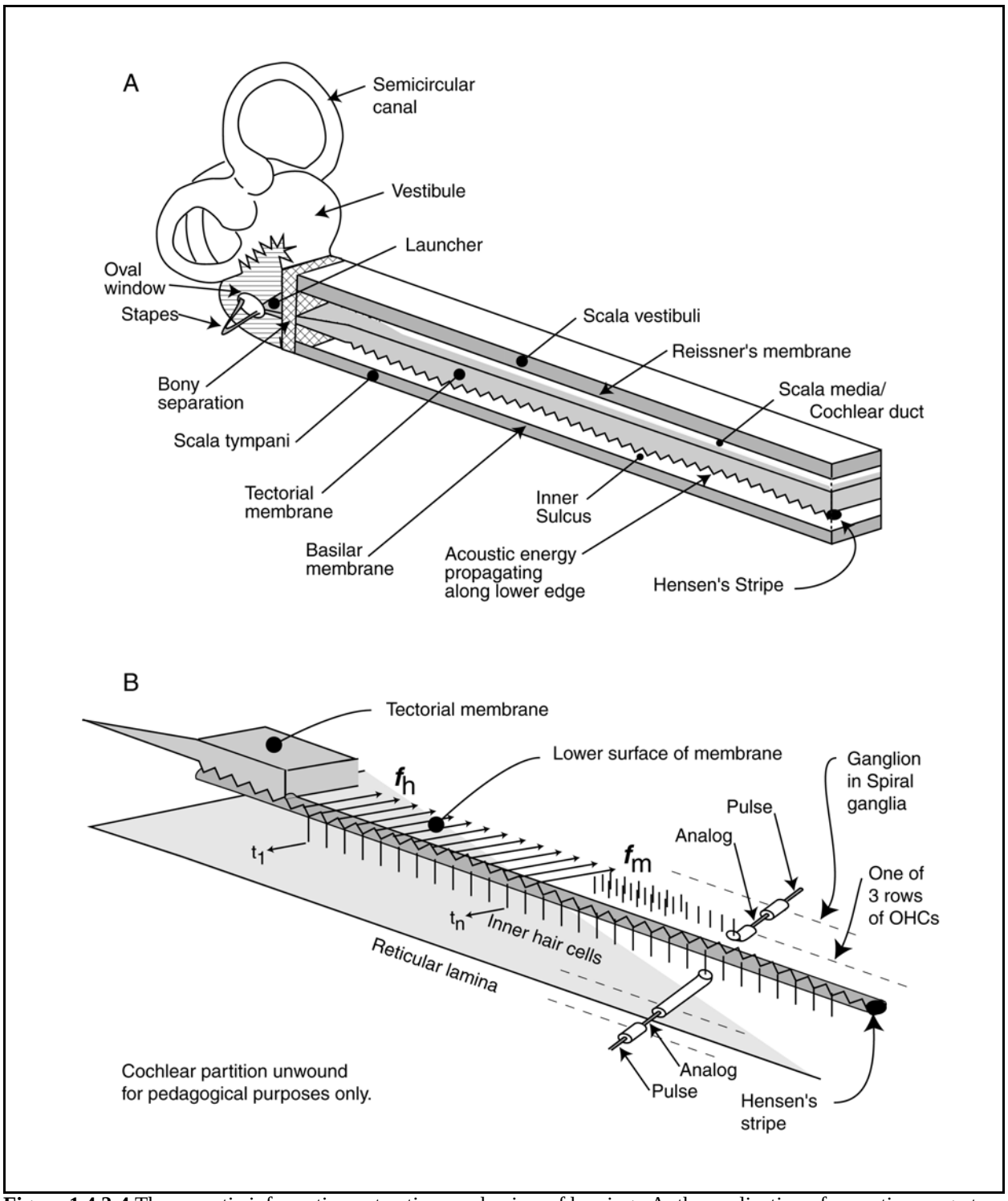


**Figure 1.4.2-4** The acoustic information extraction mechanism of hearing. A; the application of acoustic energy to the SAW filter of the tectorial membrane. The perilymph filling the scala vestibuli and the scala tympani does not participate in the primary acoustic processes. The primary mechanisms are immersed in the endolymph. The launcher portion of Hensen's stripe is excited within the vestibule of the labyrinth by energy propagated from the stapes and oval window. B; the transfer of the extracted energy to the neural system. Two separate types of signals are generated by the inner and outer hair cells. When coiled, the energy transfer into these channels is a function of the curvature of Hensen's stripe.

### 1.4.2.4.1 The dispersion of the received energy within the cochlea of dolphins

As developed in Chapter 4 of "Processes in Biological Hearing," the nominal curvature of Hensen's stripe is given by a mathematical formula known as a Hankel function. This function describes the complete frequency-position-delay characteristic for a given mammalian species. As noted earlier, many mammals exhibit an increase in curvature (decrease in local radius) near the apex of the cochlea. The dolphin appears to be one of these species. **Figure 1.4.2-5** illustrates a typical cochlear partition from a bottlenose dolphin overlaid by a Hankel function. The parameters of the Hankel function are Start = 2.0, End = 15.4 and Hook parameter = 18. The figure introduces something of an optical illusion due to the variation in the width of the solid line representing the cochlear partition. The dashed line is a simple mathematical function with a smoothly varying curvature. It is the cochlear partition that is somewhat irregular.

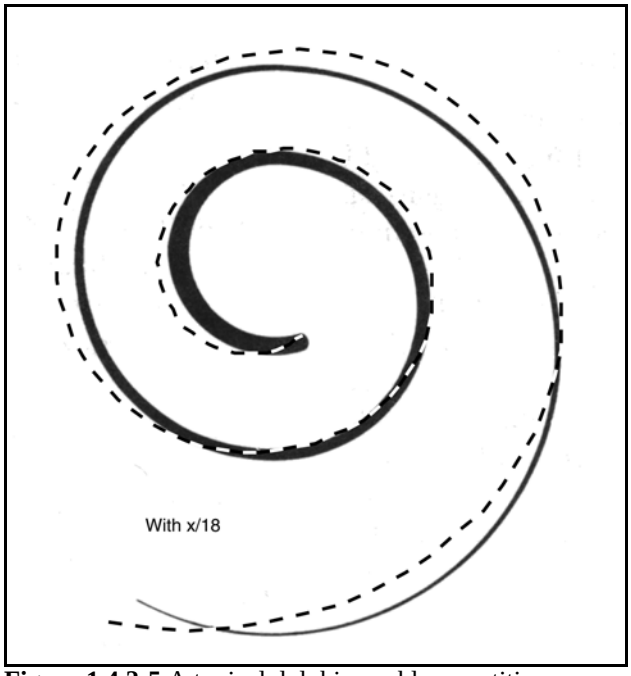


**Figure 1.4.2-5** A typical dolphin cochlear partition overlaid by a Hankel function. See text. Dashed curve is Hankel function for 2<x<15.4. Solid curve from McCormick, 1971.

The agreement between the measured shape of the cochlear partition from a single bottlenose dolphin without range bars and the theoretical Hankel function appears excellent. The variation is well within the range found in other species, including humans. The variation suggests the animal had some deviations from what one might call "hearing with a linear variation in frequency with position" If one plots the local radius of curvature (an approximation to the true curvature of a Hankel function) and scales it properly, one obtains the frequency place characteristic for this species. **Figure 1.4.2-6** shows this characteristic, using the conventional scales of hearing research log-log scales, for the nominal bottlenose dolphin cochlea described by the above Hankel function. The abscissa corresponds to the distance along the cochlea from its initial point within the vestibule of the labyrinth to its terminus at the helicotrema. The ordinate scale represents the frequency range to which the species is sensitive. The precise center frequency of the first and last set of outer hair cells in the cochlea of the dolphin are not known. However, a scale from 150 Hz to 150 kHz is frequently assumed for the bottlenose dolphin. These limits do not necessarily correspond to the limits of the sensitivity spectrum shown in the next section. This figure also shows the relative delay to be expected, assuming the velocity of propagation along the stripe is six meters/sec. This delay is important in describing the neural network of the dolphin later in this work.

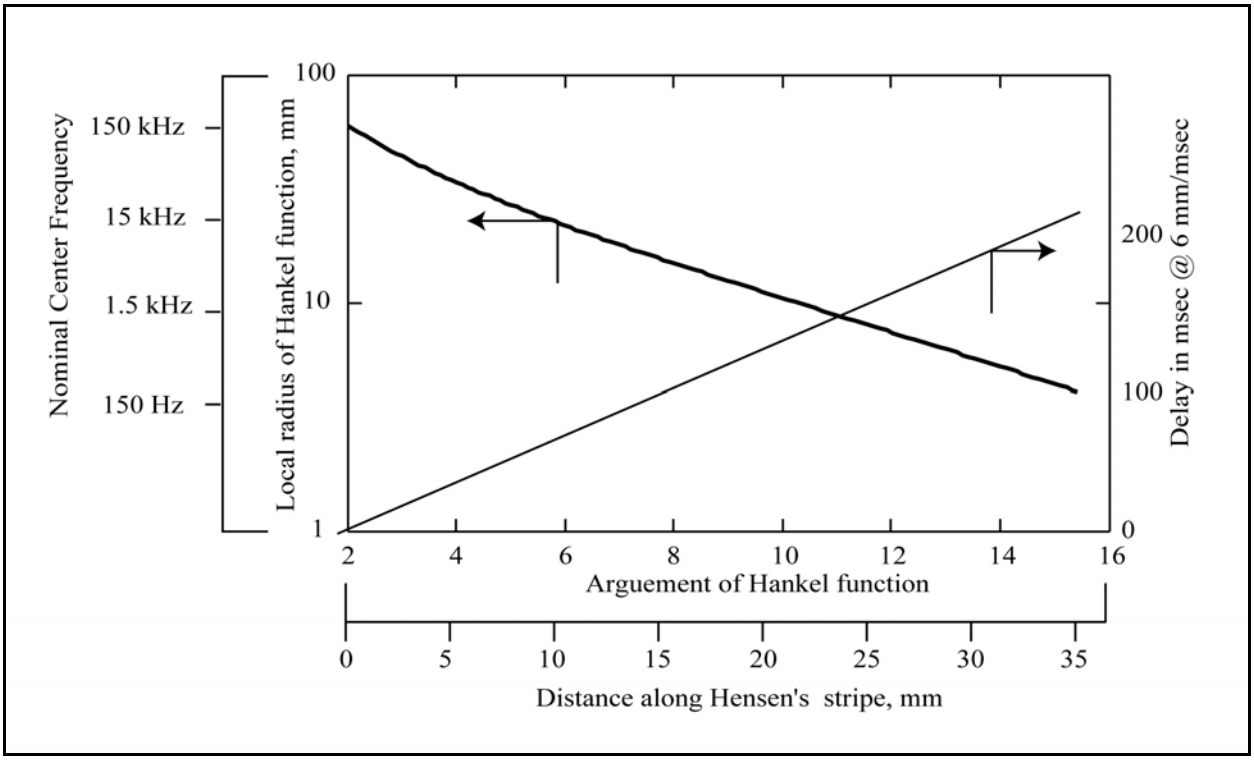


**Figure 1.4.2-6** Performance parameters for Hensen's stripe for the nominal dolphin cochlea.

### 1.4.2.4.2 Initial signal generation by phonoreceptors in the dolphin

The generation of the initial signals by the hair cells of the dolphin cochlea can be assumed to be like that of all other mammals explored to date.

The arrangement of both the inner and outer hair cells along the basilar membrane and their contact with the tectorial membrane is virtually identical to that found in the human. As a result, both the temporal signals associated with the inner hair cells and the tonal signals associated with the outer hair cells can be expected to be generated in the same manner.

### 1.4.2.4.3 Energy vs phase sensitivity of the signal generation mechanism

Some data is available that limits consideration of the dolphin receiving system as an energy detector. In addition, the binaural sensitivity of the dolphin at low frequency, like that of the human, is not compatible with a simple energy detector.

Supin & Popov have reported on the sensitivity of the receiving system to the variation in the shape (based on phase changes) of the envelope of individual pulses but on a global basis[127]. The global basis involved the measurement of evoked potentials measured at the surface of the animals head. They assert these signals can be described as auditory cortical responses due to their similarity to auditory brainstem responses. Strictly speaking, such phase sensitivity is not compatible with an energy detector.

The performance of the tonal and temporal channels of hearing should be examined separately, and then from a binaural perspective, to define the phase performance of the overall system adequately.

Chapter 5 of "Processes in Biological Hearing" describes the phase sensitivity of the sensory neural channels at frequencies below 600-3,000 Hz depending on the species. Below this frequency, the binaural signals projected to the inferior colliculus are compared on a phase basis. Below this frequency, the detection system can only be considered an energy detector on a very short term basis. Above this break frequency, the sensory neurons operate as nearly perfect integrators, and can thus be described as energy detectors.

### 1.4.2.5 Composite performance of the dolphin

Several performance parameters of the dolphin can be deduced from only the above discussion of only the physiological and neurological elements of its hearing.

### 1.4.2.5.1 The limiting auditory sensitivity of dolphins

**Figure 1.4.2-7** compares the acoustic sensitivity of the dolphin and the human[128]. While the absolute sensitivity is higher due to the larger collection apertures of its "outer ears," it also achieves a considerably higher ultimate frequency.

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[127]Supin, A. & Popov, V. (1989) Frequency-selectivity of the auditory system in the bottlenose dolphin, *Tursiop turncatus in* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pp 385-393

[128]Johnson, S. (1967) Sound detection thresholds in marine mammals *In* tavolga, W. *ed*. Marine BioAcoustics NY: Pergamon Press pp 247-260

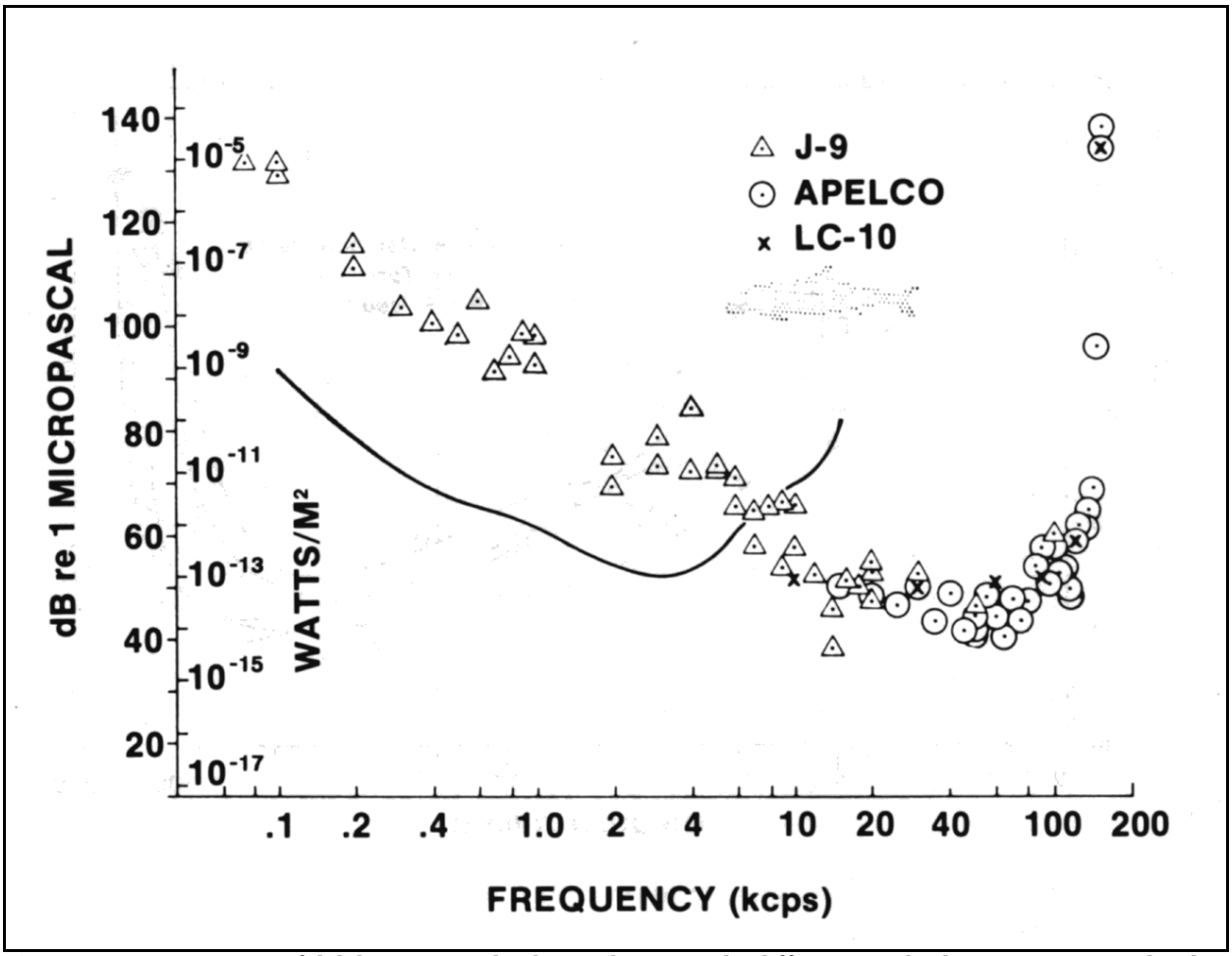


**Figure 1.4.2-7** Sensitivity of dolphin compared to human hearing. The difference in absolute sensitivity is related to the larger receiving aperture of the outer ear. From Johnson, 1967.

### 1.4.2.5.2 The frequency discrimination capability of the dolphin

Based on the geometry of the cochlea in the dolphin, the frequency discrimination capability of the cochlea is $f_{max}/f_{min}$ = (min. step)$^{3500}$ before considering any rolloff in frequency response due to other factors. For $f_{max}$ = 150 kHz and $f_{min}$ = 200 Hz, the minimum step is 1.0019 or slightly less than two tenths of 1percent (~0.2%) of the characteristic frequency. This value is 28.5 Hz at 15,000. This value will be reduced by any diffraction within the dispersion mechanism and the finite size of the outer hair cells. It may also be reduced by any longitudinal summation of the signals from adjacent outer hair cells. It could be increased by interpolation within the signal manipulation process but this is unlikely because of the automatic gain control built into the sensory neurons. This percentage value is very close to the mid band values reported by Au (1993, p. 41) and shown in **Figure 1.4.2-8**.

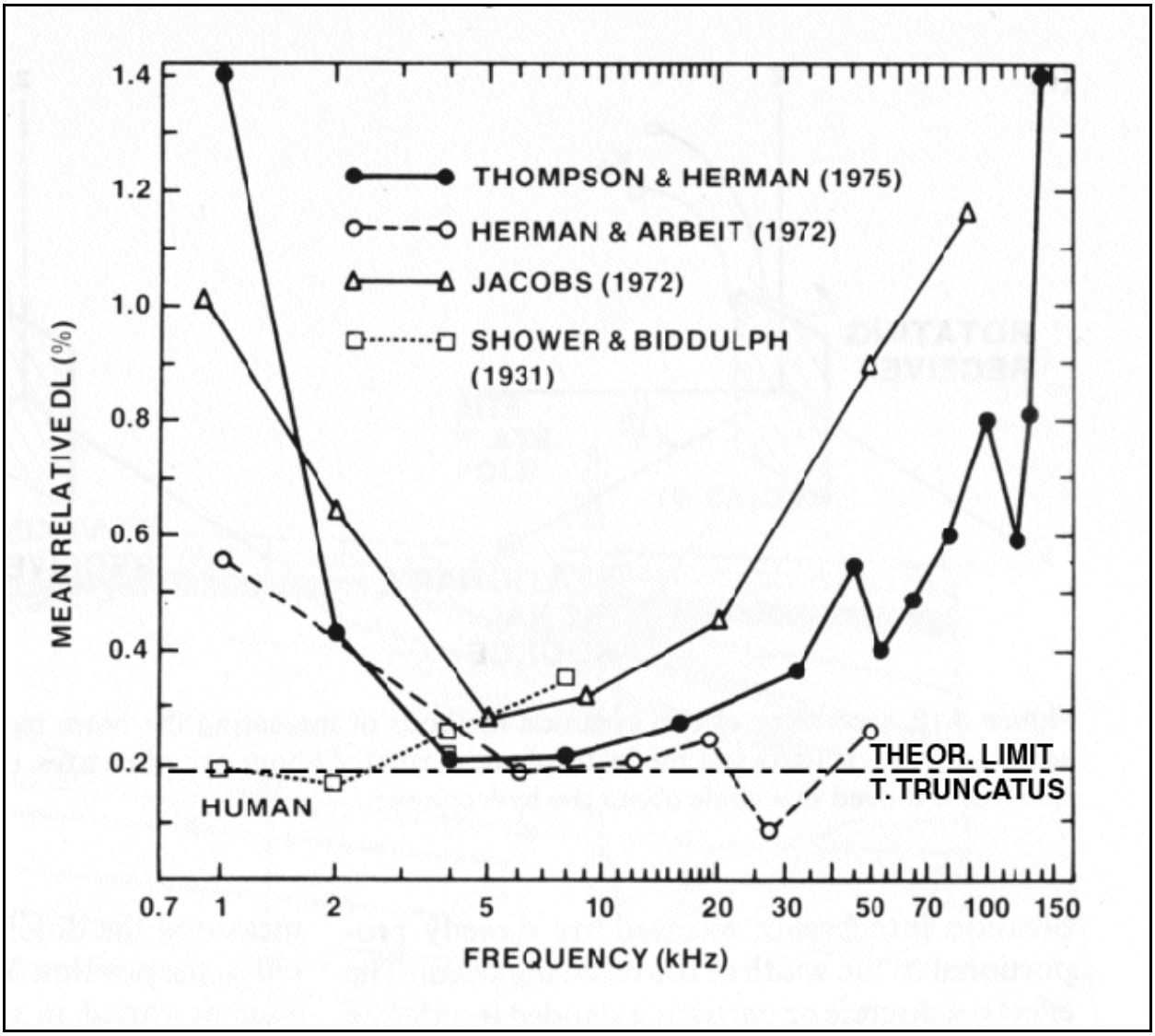


**Figure 1.4.2-8** Frequency difference threshold for the bottlenose dolphin and humans. Theoretical limit is based on this study and applies to the swept continuous tone echolocation capability (generally below 30 kHz). Other data from Thompson & Herman, 1975.

The above discussion strongly suggests the whistles of the bottlenose dolphin are due to their use of a swept continuous tone Doppler radar for echolocation in the range of 100 to 600 meters and that this system achieves near theoretical performance within this range.

A problem appears in the 1993 book by Au. The apparent excellent frequency discrimination provided by the cochlea stands in stark contrast to Au's statement on page 122 based on a paper by Thompson & Herman[129]. Au claims the bottlenose dolphin cannot perceive frequency

[129]Thompson, R. & Herman, L. (1975) Underwater frequency discrimination in the bottlenose dolphin and the human *J Acoust Soc Am* vol 57, pp 943-948

differences of better than 8 kHz in the 100 to 130 kHz range. The problem appears to originate in the reading of figure 2 of Thompson & Herman. The ordinate scale includes a factor of $10^3$. However, the scale is a ratio relative to 100,000 Hz. The absolute value of the difference limen expressed as a differential frequency threshold is 800 Hz (in agreement with Table I of the Thompson & Herman paper). Au actually reproduces figure 2 of Thompson & Herman on page 41 and draws the correct conclusion that the limiting limen is near 0.2% (285 Hz at 15 kHz), rising to near 800 Hz near the edge of the effective operating range.

### 1.4.3 Signal processing & signal propagation in dolphins

This section stands as a placeholder. Virtually nothing is known about the signal processing performed in the neural system of the dolphin between the signal generating phonoreceptors of the cochlea and the CNS, other than some counts of the number of neurons exiting the spiral ganglia. Signal propagation in the dolphin appears analogous in every way with that discussed in Chapter 7 of "Processes in Biological Hearing."

The spiral ganglia of the dolphin is homologous with that of other mammals. No references were found in the literature detailing the spiral ganglia adjacent to and intertwined with the cochlea. It is known to create about three times the number of ganglion output cells as found in the human spiral ganglia. Precisely where these neurons extend to within the cochlear nucleus is unknown in 2006. The general physiology associated with the spiral ganglia can be found in Chapter 6 of "Processes in Biological Hearing."

Very little is known about the neural system of the dolphin at the detailed level. The most prominent feature is the physical cross section of some of the neurons emanating from the spiral ganglia. While the literature has asserted that this would make the signal propagation somewhat faster based on the chemical theory of the neuron, the situation is more complex. Based on the electrolytic theory of the neuron, underpinning this work [Chapter 14 of "Processes in Biological Vision," www.sightresearch.net/pdf/14Tertiary.pdf ], both the bandwidth and the average propagation velocity of neurons are determined primarily by the characteristics of the Nodes of Ranvier that occur along the length of propagation neurons. The diameter of an axon is a secondary factor. The highest bandwidth neurons previously reported in mammals are found in the neurons involved in the phase comparison circuits used in defining the direction to a source and possibly in neurons of the precision optical servo system (POS). This maximum is near 600 Hz. It is possible some of the neural paths emanating from the spiral ganglia neurons in the dolphin could exhibit bandwidths up to about 1,000 Hz may be present. The actual value of this parameter is important in delimiting the performance of the echolocation circuits of the dolphin discussed below.

The very general comments predicting the size of the axons in various neural paths based on time delays encountered within the system do not reflect a detailed understanding of the neural system. Much of the delay encountered at different locations within the brain is due to the time allotted to signal manipulation in one or more of the neural engines (generally described as independent nuclei or areas of the cortex surface in the morphology literature) rather than due to variations in size of the interconnecting signal projection neuron.

Ridgway has discussed briefly the diameter of the neurons emanating from the spiral ganglia[130]. He reports those between the spiral ganglia and the lateral lemniscus to be as large as 12 microns in the bottlenose whale, *Hyperoodon ampullatus*, with diameters of at least seven microns in the bottlenose

[130]Ridgway, S. (2000) The auditory central nervous system of dolphins In Au, W. Popper, A. & Fay, R. eds Hearing by Whales and Dolphins. NY: Springer pg 279

dolphin.

## 1.4.4 Signal manipulation and cognition in dolphins

Some excellent studies of the anatomy of the dolphin brain have been published. However, very little work has been published on the morphology of the brain in dolphins compared to that for bats. **Figure 1.4.4-1** shows the remarkable similarity between the brains of the dolphin and man. The figure was used recently as a frontpiece in Swanson[131].

Only brief physiological studies have been made into the neural system of the dolphin. Most of the data has been obtained with non-invasive procedures, such as auditory brainstem responses (ABR). The analysis of the resulting data has been quite limited, mostly to comparing waveforms with those of other species.

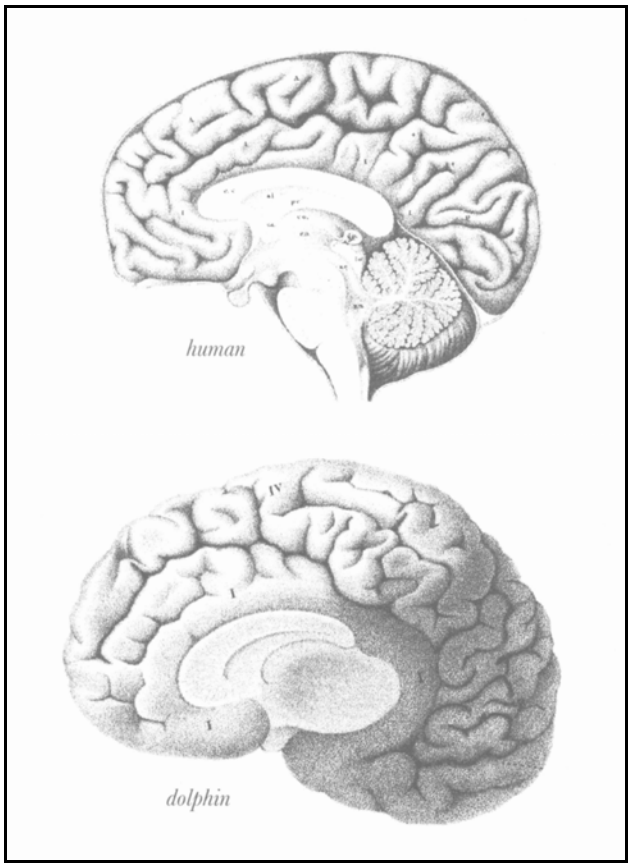


**Figure 1.4.4-1** A comparison of the right medial brain of dolphin and human drawn to the same scale. The brainstem and cerebellum of the dolphin have been removed for clarity. From Leuret & Gratiolet, 1857.

The analysis of waveforms such as those by Ridgway in Au, Popper & Fay (p. 286) and in Leatherwood & Reeves (p. 91) can proceed much farther if the origins of the various components of the auditory brainstem response (ABR) are better understood. The reader is referred to Fulton (2005, Sec 11.1.6) for additional information on this subject. The information is applicable to both the visual and auditory sensory domains.

This section will assume the neural system of the dolphin is typical of other mammals with the primary differences being in ecologically defined optimizations in specific portions of the brain. As an often quoted example, the eye sight of dolphins cannot be relied upon in murky water. As a result, the dolphin has optimized its phonic and auditory capabilities to provide an alternate high spatial resolution capability. The visual portions of its brain, both occipital lobe and the visual part of the diencephalon appear less developed than in humans. It has been reported that the dolphin has no fovea in its retina. However, this statement needs further confirmation.

Nearly all of the studies related to the neural system and brain of the dolphin must be considered as statistically inadequate and only representing a unitary or very small sample group.

[131]Swanson, L. (2003) Brain Architecture. NY: Oxford Univ Press Frontpiece

The model presented in Biological Vision[132] and the similar model presented in Biological Hearing[133], both by Fulton, suggests a framework for analyzing both the passive and active auditory capability of the dolphin. The figure in **Section 1.1.2** above will be expanded in the following discussion.

### 1.4.4.1 The gross morphology, homeostasis and vascular circulation

#### 1.4.4.1.1 The evolution of the stage 0 elements of the dolphin auditory modality

The stage 0 (pre-neural) portions of the auditory modality of the dolphin went through a variety of evolutionary changes over the last 50 million years. The most important from the echolocation perspective was the isolation of the bony structure enclosing the inner ear from the skull in order to functionally isolate the sound receiving system from the reverberations associated with the sound generating system. Thewissen, in a book written for a popular audience, summarized the major changes in **Figure 1.4.4-2**. His interpretative remarks rely upon a few concepts that he assumed to be true. A part of his figure has been omitted in this figure because bone conduction plays no role in dolphin hearing or echolocation. In fact the separation of the bulla from the skull and the introduction of a large number of air sacks around the bulla are designed to minimize bone conduction. The lower jaw bone plays no role in dolphin hearing as discussed and illustrated in **Section 1.1.3.1**.

Figure 66 of Thewissen provides an even wider cladogram (with time scale) of the whales and their association with the artiodactyls (even-toed ungulates).

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[132]Fulton, J. (2004) Biological Vision: A 21st Century Tutorial. Victoria, BC, Canada: Trafford. ISBN 141201917-6

[133]Fulton, J. (2006c) Hearing: A 21st Century Paradigm. Victoria, BC, Canada: Trafford, ISBN 142516065-4

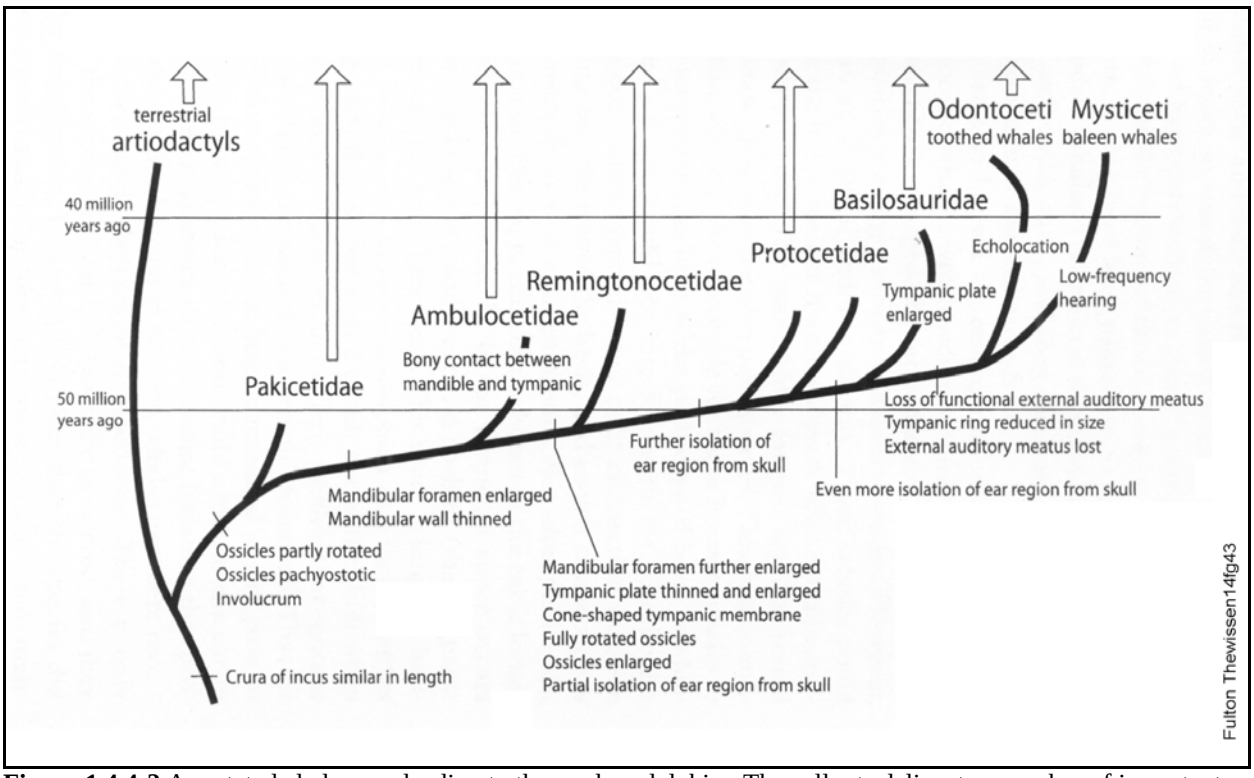


**Figure 1.4.4-2** Annotated cladogram leading to the modern dolphin. The callouts delineate a number of important changes in the configuration of the stage 0 elements of the dolphin auditory modality. They begin with the significant changes in the ossicles, significant isolation of the bulla from the skull and mellon, loss of function via the meatus of the external ear, and the implementation of significant echolocation capability. See text. .From Thewissen, 2014.

Figure 44 of Thewissen, from Nummela et al[134]. suggest the size of the tympanic plate of whales is an order of magnitude larger than the eardrum of equivalent size terrestrial animals. This feature, along with the size of the external ear adjacent to the lower jaw, are suggestive of the ultimate sensitivity of the dolphin hearing system.

### 1.4.4.1.2 The morphological arrangement of the auditory engines of the dolphin brain

Zook, et. al. have reviewed the available morphological material up to 1986[135]. Their discussion does not progress beyond the concept of a filter as a black box. Some cytology of the brain has been published but it is mostly in superficial form and not tied closely to the physiology of the system. Morgane, Jacobs & Galaburda, in chapter 5 of Bryden & Harrison, have provided some information

[134]Nummela, S. Thewissen, J. Bajpai, S. Hussain, T. & Kumar, K. (2007) Sound transmission in archaic and modern whales: anatomical adaptations for underwater hearing *Anatom Record* vol 290, pp 716–733

[135]Zook, J. Jacobs, M. Glezer, I. & Morgane, P. (1986) Some comparative aspects of auditory brainstem cytoarchitecture in echolocating mammals *In* Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pp 311-316

on the cytoarchitecture of the brain of *Cetacea*[136]. Their focus was on the neocortex to the exclusion of the diencephalon and other elements of the paleocortcx. They note the difficulty in comparing the brains of Cetacea with Hominoidea because of the distinctly different ecological niches and resultant neural evolution. They suggest reverting back down the phylogenic tree to find a common ancestor and performing comparisons beginning from that base.

They do note, "since from the outset it is clear that cortical architecture in the primate brains is strikingly different from that of the whales" (p. 84). The differences appear to relate to both the laminar organization of the neocortex and the cell populations within those layers. The neocortex is probably the least important part of the bottlenose dolphin brain (except for the frontal lobe) when discussing echolocation. Morgane & Glezer have also written on the morphology of the neocortex[137]. They went farther and discussed the cytology of some areas of the neocortex.

Morris has noted the unusual vascular system in dolphins and its potential utility in connection with deep diving as well as thermal control and possible dampening of vascular pressure variations[138]. Houser, et. al. have performed a broader set of *in-vivo* studies using medical imaging equipment to provide significantly more information in this area[139]. The studies provided significant new information in several areas. The role of the vascular circulation in maintaining uniform temperature within the fat tissue representing the beam forming elements of both the transmitting and receiving portions of the echolocation system was emphasized. The role of the air sacs in surrounding the bulla of the ears and providing acoustic isolation from the nearby transmitting elements was emphasized. Additional details concerning the pneumatic pathways within the head were also provided.

Ridgway has also provided brief discussions of the brain of the bottlenose dolphin[140],[141]. He also notes the apparent ability of the animal to achieve a sleep-state in only one-half of the brain at a time. Although able to sleep with both eyes closed[142], the animal is known to enter a sleep-state with one eye remaining open at a time. Ridgway did not discuss the importance of the paleocortex to echolocation and other specialized capabilities of the dolphin. Ridgway did note the fact the pinna is lacking in dolphins and the earlier comment of McCormick that the malleas of the middle ear does not attach directly to the tympanic membrane.

Unfortunately, the above presentations did not describe the paleocortex and neocortex or present

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[136]Morgane, P. Jacobs, M. & Galaburda, A. (1986) Evolutionary apects of cortical organization in the dolphin brain *In* Bryden, M. & Harrison, R. *eds*. Research on Dolphins. Oxford: Clarendon Press pp 71-98

[137]Morgane, P. & Glezer, I. (1990) Sensory neocortex in dolphin brain *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pp 107-136

[138]Morris, R. (1986) The acoustic faculty of dolphins *In* Bryden, M. & Harrison, R. *eds*. Research on Dolphins. Oxford: Clarendon Press chap 18

[139]Houser, D. Finneeran, J. Carder, D. et al. (2004) Structural and functional imaging of bottlenose dolphin (Tursiops truncatus) cranial anatomy *J Exp Biol* vol 207, pp 3657-3665

[140]Ridgway, S. (1990) The Central Nervous System *In* Leatherwood, S. & Reeves, R. *eds*. The Bottlenose Dolphin. NY: Academic Press pp 70-77

[141]Ridgway, S. (2000) The auditory central nervous system of dolphins In Au, W. Popper, A. & Fay, R. eds Hearing by Whales and Dolphins. NY: Springer pp273-293

[142]Ridgway, S. 1995) Dolphin Doctor, 2nd Ed. San Diego, CA: Dolphin Science Press pg 47

imagery showing the posterior dorsal aspect. Bullock & Gurevich have provided a broader range of details of the CNS of the bottlenose dolphin based on early studies in the Soviet Union[143]. They highlight the significant differences in size between the elements of the paleocortex in the dolphin, the bat, and in humans. They note particularly the "prodigiously large" size of the lateral lemniscus of dolphins, including a nucleus unknown in humans. They make similar observations concerning the inferior colliculus (p. 62). Beginning on page 59, they discuss aspects of both the dorsal and ventral cochlear nuclei.

**Figure 1.4.4-3** reproduces a crucially important table derived from Zvorykin by Bullock & Gurevich. It has been expanded to stress the massively larger acoustic elements of the brainstem of the dolphin compared to the human, on both an absolute volume basis and relative volume basis using the weights in column 15. This contrasts with the visual components shown that are only marginally larger. It also contrasts with the relatively smaller cerebral cortex of the dolphin compared to the human (not shown).

TABLE I

VOLUMES OF AUDITORY AND VISUAL STRUCTURES IN THE BRAINS OF DOLPHINS (*Delphinus delphis*), BAT (*Pipistrellus pipistrellus*), AND MAN (*Homo sapiens*), IN CUBIC MILLIMETERS[a]

| | Auditory | | | | | | | | | | Visual | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| | nuc. cochl. dors. | nuc. cochl. vent. | oliva super. | nuc. trapez. | nuc. lem. lat. vent. | nuc. lem. lat. interm. | nuc. lem. lat. dors. | collic. inf. | corp. genicul. med. | sum, 1 to 9 | collic. sup. | corp. genicul. lat. | Sum 11 + 12 | Ratio 10:13 | Brain weight (gm) |
| Dolphin | 7.0 | 160. | 150. | 85. | 217. | 160 | 40 | 470 | 340 | 1629 | 108 | 143 | 251 | 6.5 | 780 |
| Bat | 0.02 | 0.23 | 0.16 | [b] | 0.04 | 0.08 | 0.02 | 1.21 | 0.22 | 1.98 | 0.50 | 0.10 | 0.60 | 3.3 | 0.5[c] |
| Man | 1.2 | 10.8 | 0.96 | [b] | 1.10 | 0 | 0.43 | 38.0 | 48.5 | 101 | 102 | 92 | 194 | 0.52 | 1250 |
| **Ratio D/M** | | | | | | | | | | | | | | | |
| **Absol. vol.** | **6.3** | **15** | **156** | **>100** | **195** | **>>160** | **9.3** | **12** | **7** | **16** | **1.0** | **1.5** | | | |
| **Rel. vol.** | **10** | **24** | **260** | **>160** | **310** | **>>260** | **15** | **19** | **12** | **26** | **1.6** | **2.4** | | | |
| **Proposed functions** | **Initial signal formatting** | | | | **Active echolocation** | | | **Passive source location (Alarm)** | **Commun. & pass. location (Aware)** | | **Motor resp.** | **Content & pass. location** | | | |

[a] Modified from Zvorykin (1963, 1971).
[b] Outline too indistinct to measure.
[c] Estimate supplied by A. D. Grinnell.

**Figure 1.4.4-3** Volumes of auditory and visual structures in the brain of dolphins (*Delphinus delphis*), bat (*Pipistrellus pipistrellus*), and man (*Homo sapiens*) in cubic millimeters. Based on Bullock & Gurevich, 1979.

The proposed activity associated with each of these components is shown below the tabulation. Except for echolocation, these labels are derived from studies of the human and terrestrial mammals. The proposal that the primary active echolocation signal manipulation area is the lateral lemniscus is based on its massive proportions and its vestigial character in humans.

No detailed discussion of the morphology of the lateral lemniscus was found in the literature

[143]Bullock, T. & Gurevich, V. (1979) Soviet literature on the nervous system and physiology of *Cetacea* *Internat Review of Neurobiol* vol 21, pp 49-109

although Zvorykin did separate it into three engines in his tabulation. It is suggested that this massive neural engine consists of many more engines, specifically a thin reticulated outer layer homologous with the dolphins PGN (and possibly the more inclusive TRN) and a massive volumetric interior homologous with the dolphins pulvinar. The former can be described as a perilemniscus or a pons reticulated nucleus (PRN), with the other engines of the lemniscus retaining their current designations. This would result in an area of the pons with a strong morphological similarity to the MGN/PGN/pulvinar couple of the thalamus.

The comment is often made that the overall size of the dolphin brain is comparable to that of the human. It is not always noted that the total weight of the adult animal is on the order of three times the size of the human.

### 1.4.4.1.3 The internal architecture of the engines of the dolphin brain

Many authors have noted the differences in the laminations of the dolphin CNS and that of other mammals. Bullock & Gurevich referenced Bogoslovskaya (1974) concerning the important features of the dolphin dorsal cochlear nucleus. They referenced Avksent'yeva (1974) who noted the fourth layer was not differentiated from the third and fifth layer in the sensory cortex.

### 1.4.4.2 The neural circuits of the dolphin paleocortex EDIT

As noted in **Section 1.4.4.1**, the paleocortex of dolphins is far more developed than that in *Hominoidea*. However, it has not been extensively studied at the histological or cytological level. Galabruda and associates have provided extensive information on the cytoarchitecture of the dolphin CNS[144].

The following sections will not be completed until the Chapters of the main work, "Processes in Biological Hearing" are perfected further. While drafts of the material in Chapters 5 through 8 are available on the website, additional material needs to be placed in them in order to properly support this Appendix. [xxx]

### 1.4.4.2.1 The functional organization of the cochlear nucleus

Zook & DiCaprio have explored the possibility that the cochlear nucleus contains one or more sets of delay lines[145]. The role of delay lines can be illustrated more completely by examining the overall signal processing system. As an example, the slow wave structure of the cochlear partition introduces a time delay between longitudinally sequential inner and outer hair cells. This delay is inherent in the place-frequency-delay characteristic of all cochleas. The resulting signals must either be processed in this echelon time structure or be realigned to a common time base through the use of delay lines prior to additional processing. In the human and other mammals studied, the echelon time structure is used within the POS, and probably within the PES, to establish the direction to targets of interest. A delay, like that introduced by the cochlear partition, is actually introduced intentionally within the POS of the visual system. The delays are then removed for further processing.

Zook & DiCaprio describe one of the neural paths between the ventral cochlear nucleus (VCN) and

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[144]Galabruda,

[145]Zook, J. & DiCaprio, R. (1989) A potential system of delay-lines in the dolphin auditory brainstem *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press

the medial nucleus of the trapezoidal body (MNTB). They note the difficulty of measuring the distance precisely and estimate its path length as between 1.0 and 2.5 cm. They also measure what they consider the differential length of the neurons along this path. This differential path is associated with the cells between the top and bottom of one set of neurons arriving at the MNTB. They report this distance varied between 3.4 to 4.5 mm in *Stenella* and 2.3 to 4 mm in *Tursiops*. While it is too early to define this set of neural paths functionally, they appear to be functionally homologous with Meyer's Loop in the visual system of mammals.

In the visual system, all of the delays are generated within the system. However, in acoustic system, the speed of sound is relatively low and appreciable transit delays occur in the external environment as well as in the neurological system, especially in the bidirectional sound travel inherent in echolocation.

Zook & DiCaprio have also discussed the massive size of the trapezoid body of the cochlear nucleus in the dolphin. The cochlear nucleus is itself massive compared to that in the human. The dorsal portion is about 10 times larger in the dolphin. The ventral portion is between 15 and 24 times larger based on the table from Zvorykin (**Section 1.4.4.1**).

### 1.4.4.2.2 The functional organization of the lateral lemniscus (Reserved)

### 1.4.4.2.3 The functional organization of the inferior colliculus

The assumption is that the source location function is concentrated in the inferior colliculus of *T. truncatus*. The challenge is to describe the inferior colliculus required to achieve the experimentally measured performance of the dolphin. It is important to recall that the only signals received at the inferior colliculus associated with high frequency ranging are stage 3 pulses describing the time of initiation and the amplitude of the envelope of the energy received at the cochlea at various frequencies defined by the dispersion properties of the cochlea. The Hankel function used in the dolphin cochlea has been modified to achieve the required spectral segregation. While many have discussed the absolute timing precision required to achieve the observed targeting performance in dolphins, the important parameter is the *relative timing precision* between the two auditory channels. As long as the two channels are well matched in performance, any absolute timing errors will tend to cancel.

To achieve the performance described above, each inferior colliculus must be able to create a multi-dimensional correlation filter that can compare frames of data received over intervals on the order of 25-50 ms, a number compatible with that found in the neurological system generally. Each frame of data must be organized in a three dimensional matrix describing the distribution of the signals received as a function of azimuth, elevation and nominal center frequency. For the resolutions described above, the matrix must be on the order of 256 bins wide in azimuth, on the order of 32 bins in elevation and on the order of 60 bins in frequency resolution (100 Hz/bin). The 60 bins in frequency resolution is adequate to cover the entire velocity range of the dolphin during a feeding attack. Even small integer multiples of these numbers for the matrix size are quite achievable. During search operations, the amplitudes of the returns are not as important as the precise time of signal receipt for a particular frequency component. Thus the amplitude stored in the matrix should be that derived from the ranging information, relative time of signal receipt relative to the average of the time of receipt of all signals within the frame time. During target selection, from within a group, the amplitude of the received signals is more important since the differential amplitude determined binaurally provides the azimuth information. Similarly, the differential amplitude determined by comparing frames acquired during target illumination by alternate vocalization sources provides the elevation information.

The proposed dolphin inferior colliculi must each manipulate the incoming signals from the two auditory channels in order to compare frames based on different vocalization sources and obtain elevation information. The inferior colliculi must manipulate the incoming signals to compare signal amplitudes during vocalization from either source to extract azimuth information. Each inferior colliculus must extract a mean time delay between the start of either vocalization and the receipt of the returning signals. It must also determine the relative time of receipt of each frequency component compared to this mean time delay. By comparing the time of receipt of each frequency component between frames acquired during the falling and the rising portions of an individual vocalization, it can calculate both the range to the individual reflection and the Doppler velocity of that reflection relative to the mean range and Doppler velocity of the total target ensemble. With the above information, the dolphin is able to generate a perception of any target ensemble in multi-dimensions that include mean range and velocity of the ensemble as well as the differential velocity, differential azimuth and differential elevation of each individual component of the ensemble within the resolution capability of the system. The required matrix algebra is easily achieved using an inferior colliculus consisting of two portions,

1. a multi-dimensional correlator formed of multiple multilayer folds of neural tissue similar to that of all elements of the mesencephalon derived from the thalamic reticular nucleus (TRN) and
2. The necessary sensing and computational circuitry similar to that found in all TRN's.

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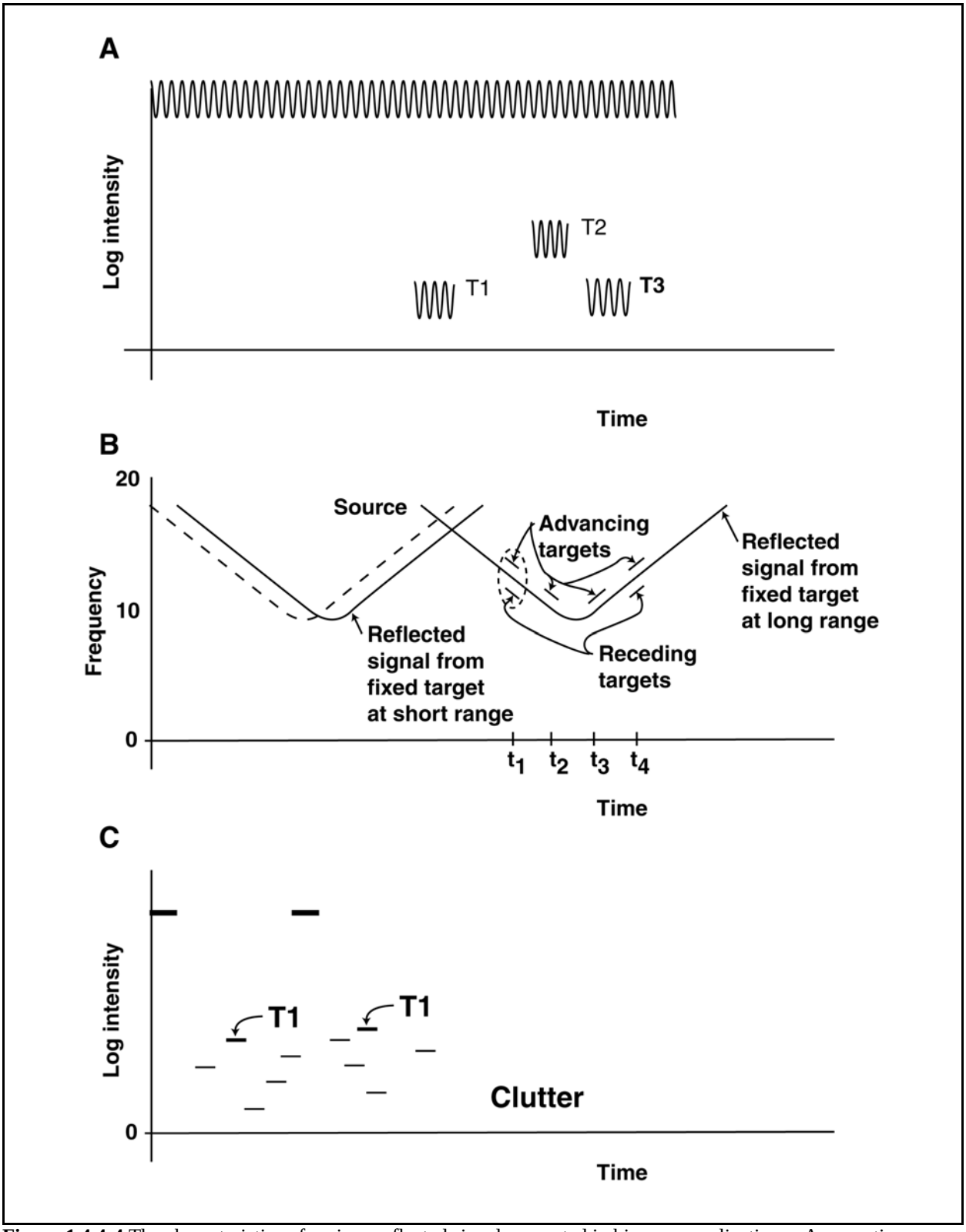


**Figure 1.4.4-4** The characteristics of various reflected signals expected in biosonar applications. A; a continuous fixed frequency signal and its reflection from three targets. B; a continuous swept frequency signal and several reflections. C; a pulse signal reflected from a target and clutter due to the background. See text.

### 1.4.4.2.4 A conceptual inferior colliculus in the dolphin

The assumption is that the source location function is concentrated in the inferior colliculus of *T. truncatus*. The challenge is to describe the inferior colliculus required to achieve the experimentally measured performance of the dolphin. It is important to recall that the only signals received at the inferior colliculus associated with high frequency ranging are stage 3 pulses describing the time of initiation and the amplitude of the envelope of the energy received at the cochlea at various frequencies defined by the dispersion properties of the cochlea. The Hankel function used in the dolphin cochlea has been modified to achieve the required spectral segregation. While many have discussed the absolute timing precision required to achieve the observed targeting performance in dolphins, the important parameter is the *relative timing precision* between the two auditory channels. As long as the two channels are well matched in performance, any absolute timing errors will tend to cancel.

To achieve the performance described above, each inferior colliculus must be able to create a multi-dimensional correlation filter that can compare frames of data received over intervals on the order of 25-50 ms, a number compatible with that found in the neurological system generally. Each frame of data must be organized in a three dimensional matrix describing the distribution of the signals received as a function of azimuth, elevation and nominal center frequency. For the resolutions described above, the matrix must be on the order of 256 bins wide in azimuth, on the order of 32 bins in elevation and on the order of 60 bins in frequency resolution (100 Hz/bin). The 60 bins in frequency resolution is adequate to cover the entire velocity range of the dolphin during a feeding attack. Even small integer multiples of these numbers for the matrix size are quite achievable. During search operations, the amplitudes of the returns are not as important as the precise time of signal receipt for a particular frequency component. Thus the amplitude stored in the matrix should be that derived from the ranging information, relative time of signal receipt relative to the average of the time of receipt of all signals within the frame time. During target selection, from within a group, the amplitude of the received signals is more important since the differential amplitude determined binaurally provides the azimuth information. Similarly, the differential amplitude determined by comparing frames acquired during target illumination by alternate vocalization sources provides the elevation information.

The proposed dolphin inferior colliculi must each manipulate the incoming signals from the two auditory channels in order to compare (bivocal) frames based on different vocalization sources and obtain elevation information. The inferior colliculi must manipulate the incoming signals to compare (binaural) signal amplitudes during vocalization from either source to extract azimuth information. Each inferior colliculus must extract a mean time delay between the start of either vocalization and the receipt of the returning signals. It must also determine the relative time of receipt of each frequency component compared to this mean time delay. By comparing the time of receipt of each frequency component between frames acquired during the falling and the rising portions of an individual vocalization, it can calculate both the range to the individual reflection and the Doppler velocity of that reflection relative to the mean range and Doppler velocity of the total target ensemble. With the above information, the dolphin is able to generate a perception of any target ensemble in multi-dimensions that include mean range and velocity of the ensemble as well as the differential velocity, differential azimuth and differential elevation of each individual component of the ensemble within the resolution capability of the system. The required matrix algebra is easily achieved using an inferior colliculus consisting of two portions,

1. a multi-dimensional correlator formed of multiple multilayer folds of neural tissue similar to that

of all elements of the mesencephalon derived from the thalamic reticular nucleus (TRN) and
2. The necessary sensing and computational circuitry similar to that found in all TRN's.

By introducing sensing neurons, where each sensing neuron, interrogates one row of a plane of the matrix, the significant features of the overall matrix can be extracted for pattern recognition purposes by subsequent engines of the brain.

The above conceptual inferior colliculus has a broad range of capabilities that appear to exhibit features commonly used in simpler species:

1. It contains the bilateral field merging feature needed in the lateral geniculate nucleus of vision to merge the half-hemisphere images from the two eyes.

2. It contains the two-dimensional planar matrix needed in the perigeniculate nuclei of both vision and passive hearing to extract specific information for pattern recognition purposes.

3. It obviously contains the individual spectral channel comparison features needed by a simpler inferior colliculus to extract the appropriate interaural time difference data (on a global basis) and interaural spectral difference data (on an individual frequency basis) required to locate the centroid of a stimulus ensemble (such as an orchestra) and the differential positions of sources within that ensemble (such as a specific instrument) based on tonal differences.

### 1.4.4.2.5 The functional organization of the perigeniculate nucleus

The topology of the medial geniculate nucleus (MGN) of the dolphin has not been elucidated to date. However, its size is indicative of its importance. It is likely that the portion of this body homologous with the acoustic perigeniculate nucleus (PGN) in the human will make up a significant portion of the dolphin medial geniculate nucleus. The perigeniculate nucleus forms a multidimensional associative memory, not unlike those found in man-made associative computer processors. It is the PGN that begins the information extraction process leading to cognition of a scene in the human.

The signals delivered to the acoustic perigeniculate nuclei of dolphins appear to be functionally equivalent to those delivered to the visual perigeniculate nuclei of the visual system in humans. This would suggest the dolphin could "image" acoustic signals in a manner that is not significantly different from what humans can do in the visual regime (except for the limitations imposed by the wavelength of the signaling mechanism and possibly background noise).

**Figure 1.4.4-5** shows the concept of the auditory signal correlation and interp extraction mechanism proposed for the human auditory system expanded to support the additional capabilities of the dolphin. The literature asserts the dolphin has approximately the same number of outer hair cells as do humans and the cochlea is very similar in length. However, the curvatures of the cochlea are different. As a result, the frequency range to which the cochlea responds is different. This is illustrated in the figure by the different slopes of the place frequency-delay characteristics on the left. Also added to the figure are the nominal frequencies supported by the active wide beam echolocation capability and the active narrow beam echolocation capability. A challenge is to determine how these additional capabilities are processed within the overall system.

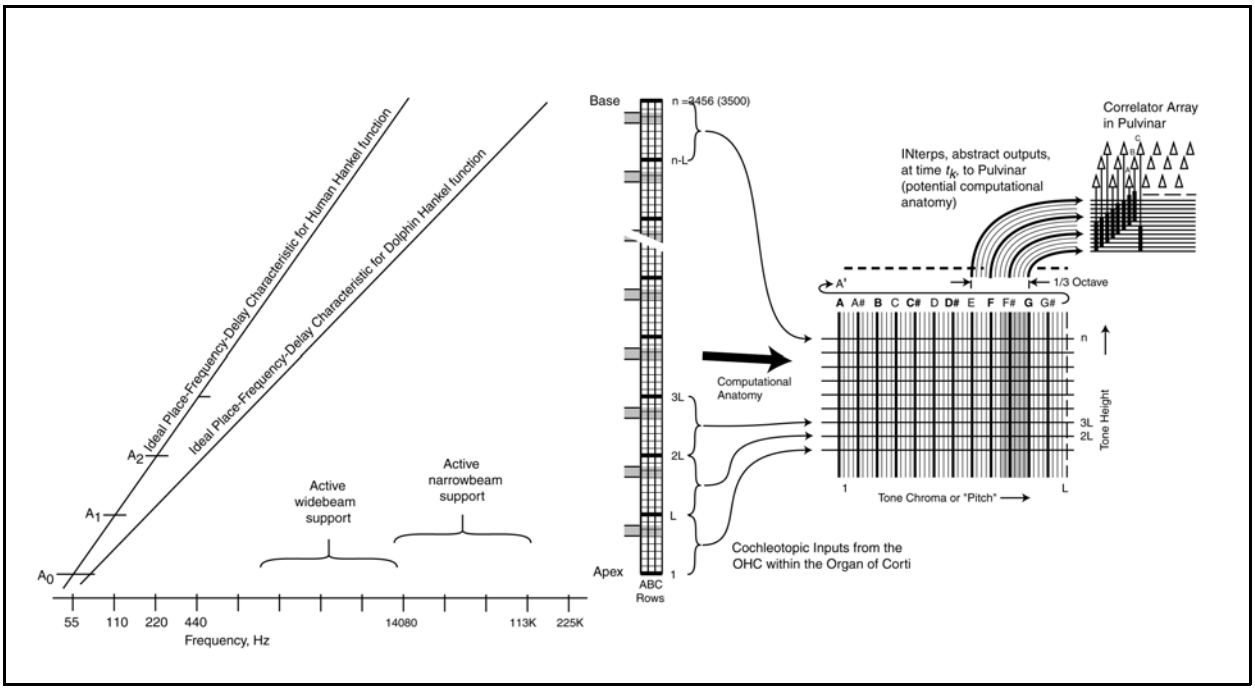


**Figure 1.4.4-5** Potential organization of the auditory analysis function in dolphins expanded from the nominal human capability. The musical notation is left on the figure for illustration. The correlator width of dolphins may differ from the correlator width (and indirectly the musical scale) of humans.

The signals from the longitudinally oriented cochlea of humans are transformed into a rectangular format by simple computational anatomy during transfer to the perigeniculate nucleus. The signals from the two cochleas are also probably merged into a single composite format prior to correlation (although this could occur subsequently with some loss in signal-to-noise ratio). The width of the array in humans is one octave.

Conceptually, the signals deposited at the nodes of the correlator are sensed by sensing neurons with long neurites contacting the columns of neurons as shown. The signals generated by these sensing neurons as a group form the first order interp extracted from the data. These interps are transferred sequentially to the pulvinar for further information extraction leading to a higher level interp. These interps are matched to patterns previously stored in the pulvinar. A successful match results in the generation of a percept, a fully resolved perception of the information supplied from the auditory system.

At first glance, it would appear the processing is likely to be very similar for dolphin hearing. Percepts could be generated from both the passive auditory system and the active echolocation system from the same basic neural architecture. It is reasonable to expect some additional neural inputs from the vocal tract describing the timing and possibly the frequency and temporal characteristics of the emitted sound. Alternately, the auditory system may be able to record a sample of the outgoing acoustic signal and use that to compare to the return signal. This information would allow the reflectance characteristics of the target to be determined as a function of frequency and time. Such frequency information would be similar to that associated with color in the visual correlation system. The timing differences would be very similar to that associated with reverberation, and incidental signal reflections, in human hearing.

On the assumption that the auditory signals of the dolphin are transferred to the perigeniculate nucleus in the same manner, the question of the width of the array arises. It is likely that the array width is also one octave in the dolphin as well. The octave organization has a particular feature in humans. Frequencies related by the exponential harmonic series, f = (base frequency)·2n where n=0,1,2 . . describe a single perceived tone that can be labeled by the notes of the musical scale. The even harmonics not represented by the exponential harmonic series and all odd harmonics generate different individual frequencies that are not consonant with the above series.

All of the exponential harmonics fall within a single vertical column in the figure. Sensing using vertically oriented sense lines is easily able to detect the note associated with the exponential harmonics. The effect is even easier to comprehend using the Spiral Tonal Map, **Figure 1.4.4-6**.

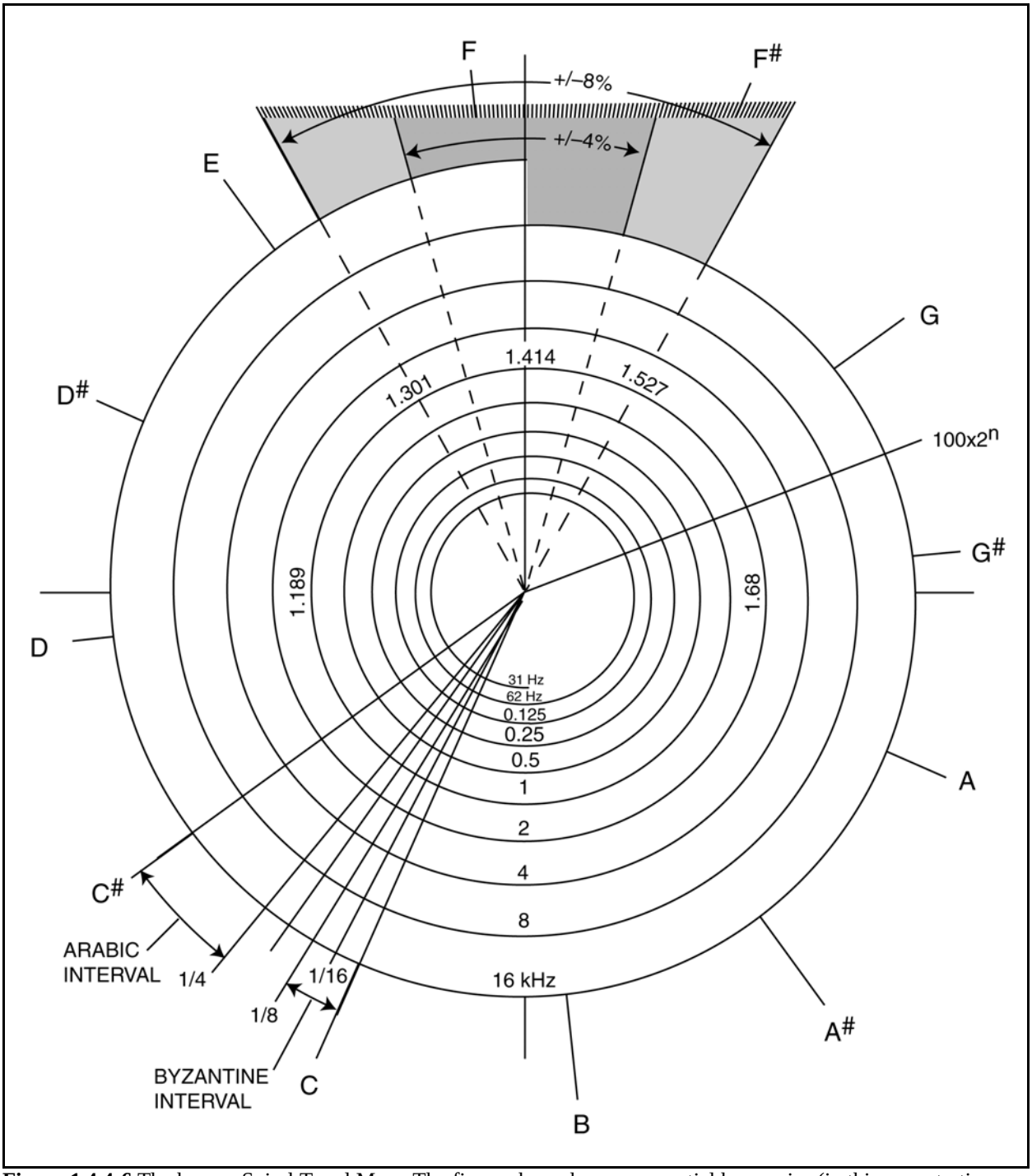


**Figure 1.4.4-6** The human Spiral Tonal Map. The figure shows how exponential harmonics (in this case starting from a base at 100 Hz at upper right) all generate the same perception of a tone. In this case, the tone is half way between G and G#. From Chapter 9 of Fulton, 2007.

By changing the curvature of the cochlea, the dolphin could use this same mapping to generate acoustic "images" quite similar to those generated by the (visual) PGN in humans and other higher mammals with a foveola. An example of this capability is shown in **Figure 1.4.4-7**. Although we do

not know the aspect ratio of the correlator in dolphin, the overall capability for the equivalent (hearing) PGN is not likely to be smaller. Thus, this figure gives a suggestion of the acoustic imaging capability of the dolphin where the minimum pixel size is probably 15 to 45 arc minutes as documented in **Section 1.5**.

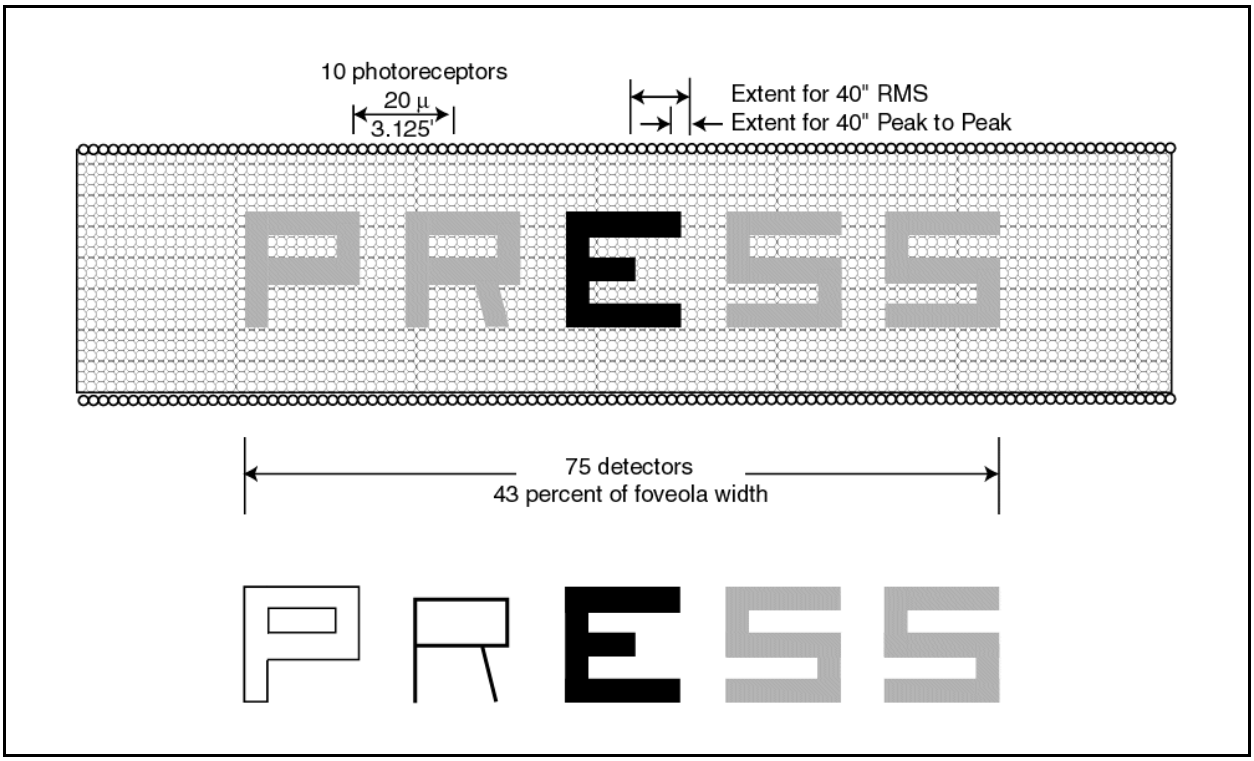


**Figure 1.4.4-7** The image map as projected onto the multi-dimensional correlator of the (visual) PGN. When projected onto the foveola, the E fills only a small part of the complete correlator space. In fact, the correlator is able to process both complete syllables simultaneously but also short words. The complete field in humans is about 150 elements wide by at least 25 elements high. From Fulton, 2004.

### 1.4.4.2.6 The functional organization of the cerebellum

Ridgway has addressed the large size of the cerebellum of the bottlenose dophin[146]. While not as proportionately large as in some species, the cerebellum of the dolphin is about 15% of the total brain mass compared to 10-11% in the human. Without a requirement for fine motor control of the digits of the hands, and less reliance on vision than in humans, the large size of the cerebellum suggests expanded powers with respect to the fine details related to hearing.

### 1.4.4.2.7 The functional organization of the cerebrum

Ridgway has also made a few remarks concerning the cerebral cortex or cerebrum of the dolphin. Little is known of its functional organization except a larger proportion of the auditory elements appear to be located on the parietal lobe rather than across the sulcus in the parietal lobe (a topographic feature of little topological importance. Morgane, et. al. have also noted the less folded

[146]Ridgway, S. (2000) The auditory central nervous system of dolphins *In* Au, W. Popper, A. & Fay, R. *eds*. Hearing by Whales and Dolphins. NY: Springer Chapter 6

character of the cerebrum compared to the human. Again a topographic feature of little topological significance except to indicate a smaller overall area for the cerebrum within a given volume.

The primary topographic feature of the cerebrum is the substantially larger area devoted to hearing than to vision.

### 1.4.4.3 The neural circuits of the dolphin neocortex

No major discussion of the organization of the dolphin neocortex, particularly as it participates in echolocation, could be found in the literature. Based on analyses by this author, the neocortex probably plays a minor role in the acquisition, interpretation and perception of information acquired by echolocation. Its role would be limited largely to the extraction of communications oriented information in the temporal lobes and cognitive functions associated with the frontal lobe of the human cortex.

The observation by Ridgway[147] of the small number of commissure in the corpus callosum is probably irrelevant in the absence of any discussion of the corpus principia within the diencephalon and the importance of the lower brain stem in echolocation.

## 1.4.5 Overall features of the system

### 1.4.5.1 Potential acoustic imaging by dolphins

Conjecture has existed for many years over whether the dolphin can form a perceptual image of an acoustic target via its high frequency echolocation capability. Comments have also been documented of some musical composers trying to describe the "image" of music they perceive during their composition activities. It is interesting to note that the human perceives full color images of his external environment using totally abstract neural signals that do not reflect the actual wavelength of the colors in the scene. The perception is developed using a visual correlator that appears virtually identical to that used in human hearing. The perception is highly dependent on the early training of the subject. Thus, the human acoustic correlator could provide an "image" of music to one highly trained in this field from a very young age. The diencephalon of the dolphin is significantly larger proportionately than that of humans. It appears entirely plausible that the dolphin, using a similar but enhanced correlator, and following its early training, could perceive an image of a distant target based on its high frequency (greater than 30,000 Hz) echolocation mechanisms. Similar conclusions can be drawn with regard to its lower frequency, wide beam echolocation capability (and even its entirely passive hearing).

### 1.4.5.2 The critical bandwidth in dolphins

The critical bandwidth characteristic provides significant support for the description of the information extraction architecture of the perigeniculate nucleus in hearing (and vision), whether used in dolphins or other mammals. The most important aspect of the critical band is that it cannot be described using a series of adjacent narrowband filters subdividing the auditory spectrum. The critical band always represents a bandwidth symmetrically placed about the center frequency of the test frequency. If the test frequency is changed incrementally, the edges of the critical band also move incrementally.

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[147]Ridgway, S. (1990) *In* Leatherwood, S. & Reeves, R. *eds*. Op. Cit. pg 76

The fundamental character of the critical band function has not been described previously in the hearing literature. That character is described in detail in Section 8.3.3 of "Processes in Biological Hearing." The critical band does not relate to a series of adjacent channels. It is always described as a bandwidth centered on the frequency of interest. As noted in **Section 1.4.2.2**, Lemonds, et. al. have provided critical bandwidth data for the bottlenose dolphin[148]. The critical bandwidth is a measure of the correlation span of the associative correlator described in the previous section and shown at the top right in the above figure. Whereas the critical band in humans spans about 1/3 octave (about 30% of the center frequency), it appears the dolphin only correlates over a span of about 15% of the center frequency. This difference probably relates to the wider frequency range of the dolphin, in terms of the number of octaves covered.

### 1.4.5.3 The variation in time coherence within the system

The measurement of absolute and relative time delays plays a major role in the echolocation system of dolphins. However, a variety of absolute and relative time delays are built into the auditory system itself. Understanding these time delays is critically important to the understanding of the systems topology and physiology. The overall system involves a multitude of time delays. The major delays when considering echolocation in dolphins are;

- associated with the finite velocity of sound in water,
- associated with the finite velocity of acoustic energy within the cochlear partition,
- associated with the finite velocity of neural signals traveling between processing engines, and
- associated with the processing time required by an individual engine.

When considering the operation of the precision echolocation servo system (PES), it is also important to consider the delays associated with the neurons and muscles associated with the sound generation system. It may also be important to understand the phase relationship between the signals produced by the two independent sources of ultra high frequency (UHF) sound available to the bottlenose dolphin.

In analyzing the performance of the auditory system of a given animal, it is often useful to develop a table of delays associated with every element in both the PES and the perceptual systems.

The neural portion of the auditory system of all mammals involves a large number of parallel neural paths. In many situations, the information is transferred in the bit-parallel, word-serial format. In many of these bit-parallel paths, the time delay associated with the individual neural paths are not the same. At a given location and time, the signals on adjacent neurons associated with the same signaling path may not apply to the same word. Such variations are inherent in the system. They begin with the slow propagation of the acoustic energy along Hensen's stripe within the cochlea at a nominal 6 m/sec (the nominal value for the human will be used in the absence of any other value). As a result of this feature, the neural signals generated closest to the apex of the cochlea occur a nominal 6 milliseconds behind the signals generated closest to the base. This variation is found in both the tonal and the temporal channels of the initial neural system.

A similar skewing of the output data occurs in the visual system where it is used to advantage. The delay, relative to the earliest signal, of visual signals in the optic nerve is directly proportional to the angular distance of the target from the line of fixation of the eye. All of the signals in the optic nerve exhibit this skewness. It is due to the relative neural path length along the curved surface of the

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[148]Lemonds, D. Au, W. Nachtigall, P. Roitblat, H. & Vlachos, S. (2000) High frequency auditory filter shapes in an Atlantic bottlenose dolphin *J Acoust Soc Am* vol 108, pg 2614(A)

retina. The angular distance to each target in the visual field is extracted within the lateral geniculate nucleus and used in both the alarm and awareness modes of perceptual operation and in the pointing and convergence operations of the precision optical servomechanism. The skewness in the signals is only removed, after the signals leave the lateral geniculate nucleus on their way to the cerebral cortex, by Meyer's loop. Both the removal of the time dispersion and its introduction involve distances of about 16 mm and signals propagating at the same velocity within the neural system.

In the binaural auditory system, the differential delay due to the difference in travel time of a signal from a target to the two ears must be considered. This differential delay is a function of both the distance to the target and the angle to the target relative to the animals sagittal plane. In addition, the significant delay introduced by the cochlear partition must be considered. The slowness of the acoustic wave within the cochlear partition is apparent in the skewed output of both the temporal channels and the tonal channels at the auditory nerve.

It is quite likely the auditory system (like the vision system) processes the neural signals data in both skewed and de-skewed forms. However, complete de-skewing of the neural signals is much more difficult in the auditory system than in vision. Using a simple delay line approach to de-skewing would require differential line lengths of about seven times the length of the cochlear partition because the acoustic velocity within the cochlear partition is at least seven times slower than in the neural system.

Zook & DiCaprio documented a de-skewing operation in the cochlear nucleus of the bottlenose dolphin[149]. They provide considerable commentary on the histology and cytology of the neurons in the ventral cochlear nucleus (VCN) and the medial nucleus of the trapezoidal body (MNTB). Unfortunately, they did not place their results in a system context. It appears the variable length of the neurons observed between the VCN and the MNTB could in the same manner as Meyer's loop in vision. While Zook & DiCaprio did not measure the time delays associated with the observed neurons, they did provide estimates of the differential length of these neural paths. They report this distance varied between 3.4 to 4.5 mm in *Stenella* and 2.3 to 4 mm in *Tursiops*. They did not describe the neurons involved in detail. However, it can be assumed they were myelinated because of their overall length which Zook & DiCaprio estimated at 1.0 to 2.5 cm. Such neurons would be expected to be myelinated, to include Nodes of Ranvier at intervals of about every millimeter or two, and operate in the phasic mode as part of the stage 3 signal propagation system. The speed of neural transmission in such neurons is typically 44 meters/sec. Thus, a length differential of 4 mm would be expected to produce a time differential of about 0.1 msec. This is a small value relative to the total delay variation associated with the cochlear partition (nominal 36 mm divided by nominal 6 m/sec = 6 msec). It would suggest the neurons observed were not associated with the auditory equivalent of Meyer's loop. Instead, they were probably performing a minor differential delay correction associated with the topography of the specific processing engines being interconnected.

Zook & DiCaprio did not present their calculations on time delay. However, they indicated calculated delays about twice as large as presented here. Such values remain small relative to those associated with the cochlear partition.

### 1.4.5.4 The auditory brain stem response

[149]Zook, J. & DiCaprio, R. (1989) A potential system of delay-lines in the dolphin auditory brainstem *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pg 181-193

The auditory brain stem response (ABR) is an evoked potential (EP) very similar to that recorded from other mammals. Ridgway has shown the ABR recorded from the Dolphin, cat, monkey and human. These waveforms are analog waveforms. They can be decomposed into the individual waveforms summed to form the ABR once the topology and physiology of the acoustic neural system is understood (Fulton, 2005, Sec 11.1.6).

## 1.5 The echolocation performance of dolphins

It is difficult to assemble a composite estimate of the performance of dolphins from data collected in a single time period. The data tend to come from different groups working at different times and locations with instrumentation appropriate to that time period.

With such a sophisticated echolocation system, it is difficult to describe the overall performance of the system without relying on many caveats and footnotes. In general, the low frequency performance and the high frequency performance are totally independent. Furthermore, the receiving system of the dolphin is difficult to model as a simple energy detector. While the inner hair cells associated with the temporal channels are primarily envelope detectors, the outer hair cells are associated with the tonal channels acting as a set of very narrow band energy detectors. The signals from these channels are then correlated using multiple techniques to achieve different objectives. This is illustrated quite clearly by the critical bandwidth associated with the dolphins hearing. This noise bandwidth is not associated with the overall bandwidth of the animal, nor is it the same fraction of the center frequency found in the human.

The maximum detection range for the dolphin echolocation system (under sea state 0), is generally estimated at about 600 meters[150]. This figure can be assumed to apply to the low frequency, low angular precision, auditory system using swept continuous tones. The angular precision would be limited to the binaural capabilities of the animal. The range precision would probably be limited to the relative intensity of the reflection and the experience of the subject.

The range for echolocation using the high frequency regime is generally about 100 meters.

Bullock & Gurevich have reported on the performance of dolphins based on the Soviet literature up through the 1970's[151]. The values from Ayrapet'yants & Konstantinov (1970) are significant but not always confirmed. They gave the data in **Table 1.5.1-1** for the bottlenose dolphin.

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[150]Morris, R. (1986) Op. Cit. Pg 388-391

[151]Bullock, T. & Gurevich, V. (1979) Soviet literature on the nervous system and psychobiology of *cetacea* *Intern Rev Neurobiol* vol 21, pp 47-87

**Table 1.5.1-1**
**Echolocation Performance of the dolphin, *T. truncatus***

| | |
|---|---|
| Discrimination of difference in distance = Threshold for 75% correct response; simultaneous presentation; distance = 1 meter or 3msec echo time. | 1.5–4 mm |
| Difference in echo time = | 2-5 μsec |
| Minimum angular separation of targets: (Cylinders; 70% correct response) | |
| Horizontal | 14 arc min |
| Vertical | 48 arc min |
| Horizontal (*D. delphis*) | 1 arc min, 40 arc sec |
| Vertical (*D. delphis*) | 1 arc min, 40 arc sec |

Au has presented data describing the range capability of the bottlenose dolphin using simple spherical metal targets and based primarily on its high precision pulse echolocation system[152]. The data has appeared in several of his subsequent writings.

Floyd has provided some performance data (primarily estimates) for the bottlenose echolocation system[153]. He has also compared that performance with two low performance man-made sonar systems.

Morris has noted an interesting additional capability of the bottlenose dolphin (p. 389). At very close ranges (well within the near-field of the high frequency echolocation system) the subject is known to approach man-made objects and encircle the object with its mouth without touching it. This appears to be a method of precisely determining the diameter of an object.

Channel 5 of the British Television System has presented a documentary in its Extraordinary Animals series (series 2, episode 4) named "The Dolphin Who Can See With His Ears." The dolphin was named Milo and has since died. It lived at the Aquarium in Belgium. Of course, the program doesn't recognize that all dolphins can image (see) with the echolocation portion of their auditory system.

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Based on its anatomy and physiology, the dolphin exhibits a very significant interaural level discrimination (ILD) capability over a nominal ±10 degrees in azimuth and ±5 degrees in elevation.

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[152]Au, W. (1989) Target detection in noise by echolocating dolphins *In* Thomas, J. & Kastelein, R. *eds*. Sensory Abilities of Cetaceans. NY: Plenum Press pp 203-216

[153]Floyd, R. (1986) Biosonar signal processing applications *In* Nachtigall, P. & Moore, P. *eds*. Animal Sonar: Processes and Performances. NY: Plenum Press pg 773-784

Based on using only constant frequency pulses, the system achieves interaural time differences (ITD) small enough to discriminate between objects with range differences of about 1-2 cm. No physiological explanation for this capability has been found yet. If a swept frequency pulse was used instead, a relatively simple explanation of this range capability is available. The frequency discrimination capability of the system is not known with precision. However, experimental results suggest the dolphin can achieve spectral segregation levels on the order of 100 Hz in the 30-150 kHz range. This range would encompass all of the Doppler velocities associated with its natural food sources. By emitting a tone burst where the tone varies in frequency between 150 kHz and 30 kHz and then returns to 150 kHz, the dolphin would be able to use this same spectral segregation level as a criteria in both range and velocity estimation calculations. The V-shaped tone burst would be similar to the observed lower frequency whistles of the bottlenose dolphin. By comparing the information between the falling and the rising portion of the return, the Doppler velocity of the target is effectively separated from the range related data. An estimate of the dolphins targeting capability is shown in **Figure 1.5.1-1**.

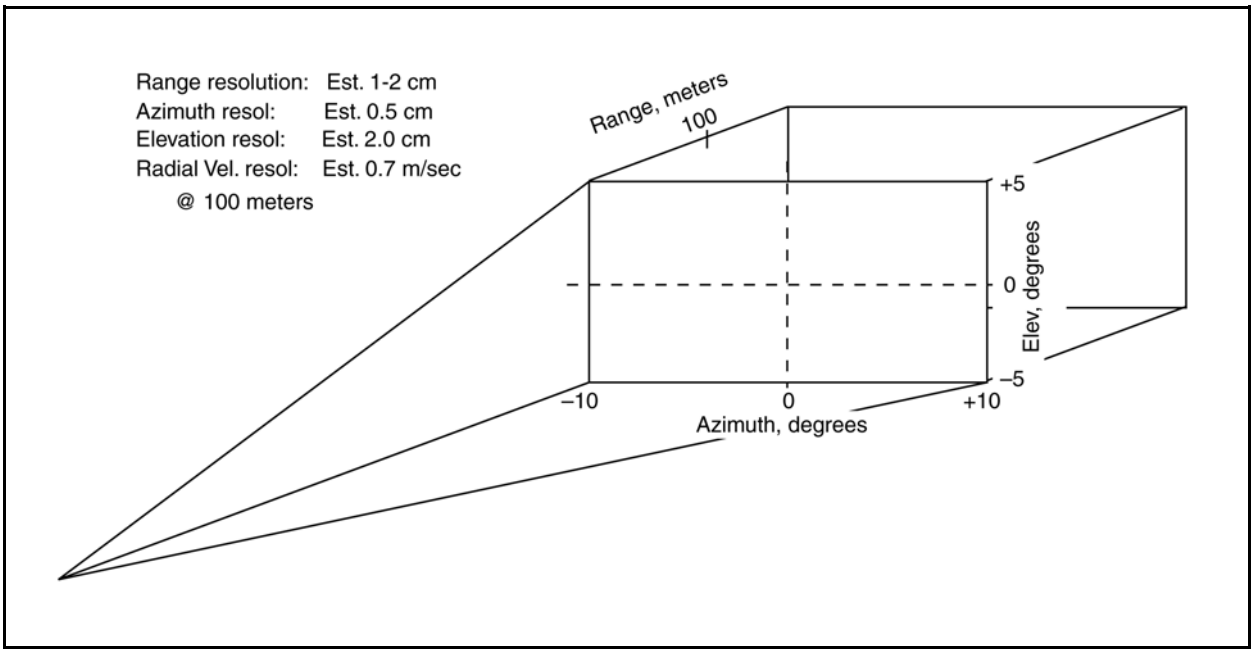


**Figure 1.5.1-1** The targeting capability of the bottlenose dolphin, *T. Truncatus* ADD.

**Figure 1.5.1-2**.shows an image of a well herded school of fish as believed to be typical of those herded by multiple dolphins before one or more dolphins makes a head-on, open-mouth attack at speed through the center of the herd. A high frequency tone emitted by the dolphin will return a well characterized Doppler frequency shift from the two sides of the ball that can be resolved by the Organ of Corti of the animal. The result would be a clear representation of the size, range and potentially the density of the herd. An estimated 0.7 meters/sec Doppler resolution would equal about 2 miles per hour. The periphery is probably moving at 5-10 miles per hour. The swim bladders of individual fish near the surface of the herd would be easily resolved at 100 meters.

It appears the best strategy for the dolphin would be to charge into the high Doppler area (approaching left flank) of the herd to capture the maximum number of fish without overly disturbing the bulk of the herd.

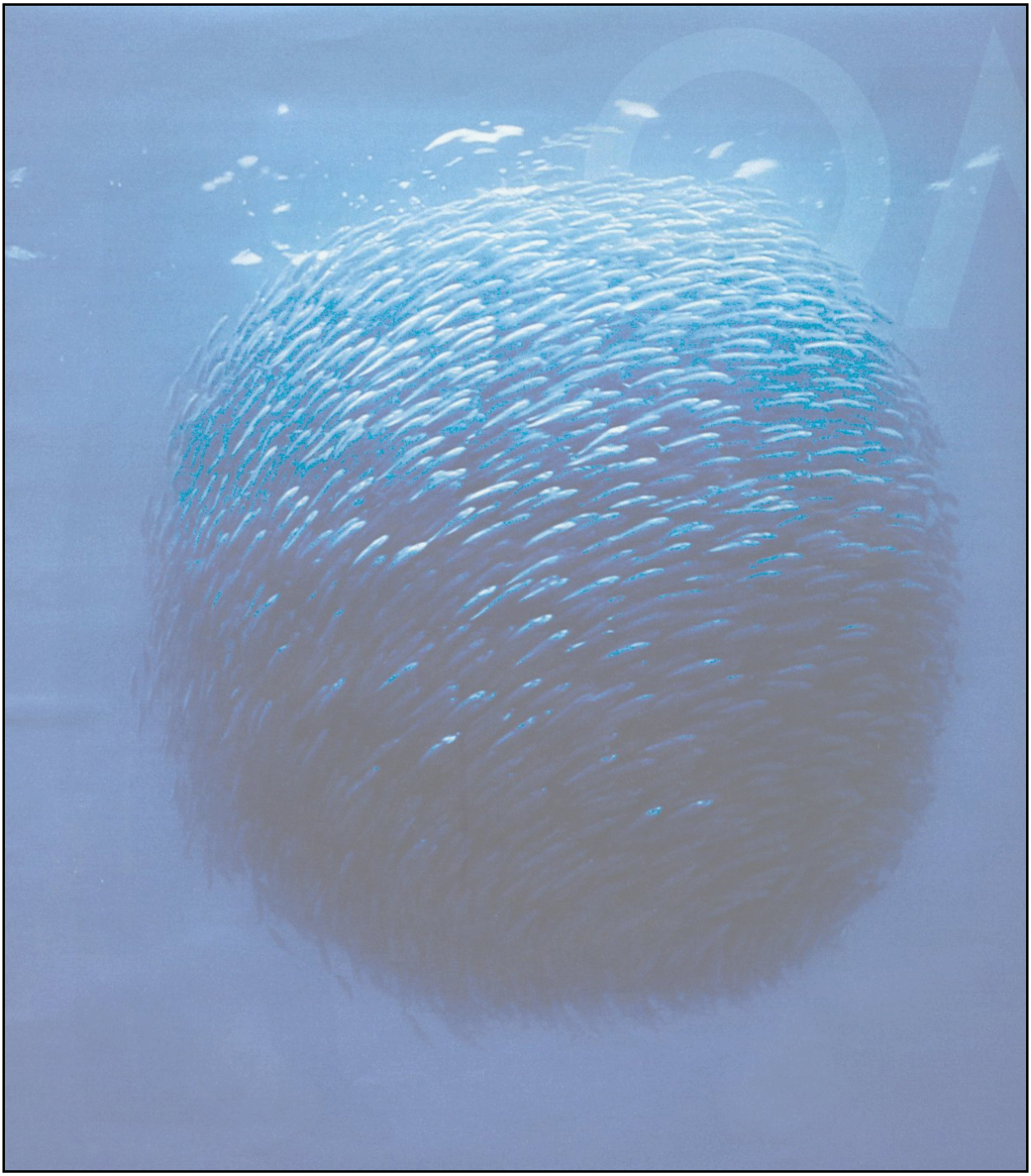

**Figure 1.5.1-2** Well herded school of fish prior to a dolphin feeding run through the middle of the ball with mouth open at speed. Note the significant difference in Doppler velocity of the sound reflected from the two sides of the ball compared to the center.

Martin et al. have developed new high performance instrumentation recently that allows a free-

swimming dolphin to be tracked in all six degrees of freedom[154,155]. The first published results are illuminating, particularly comparing the different strategies used by dolphins in an obviously inadequate experiment planned by humans. The dolphins took shortcuts not anticipated by the planner. Their spectrograms show the wide range of non harmonic frequencies employed simultaneously during the hunt for a familiar instrumented target. The authors suggest the use of two independent click sound generators simultaneously. This author notes the simultaneous generation of multiple non-harmonic lower frequency sounds in the 20-40 kHz range (which are labeled clicks in these papers but may not be based on spectrographs such as those of Boisseau in discussed in **Section 1.8.7**.

### 1.5.1 Energy conservation in echolocation

The widely reproduced data of Au (1980) shows that the bottlenose dolphin employs a power conservation strategy in its UHF signaling similar to that in modern cellular telephone systems[156]. The transmitter power is reduced following receipt of the first echo to a level that is optimal for internal signal processing. The goal appears to be the same, minimize potential interference and reverberation while maintaining adequate signal-to-noise ratio.

### 1.5.2 Bistatic echolocation operation among dolphins

Gregg et al[157]. have recently discussed bistatic sonar operation by multiple dolphins (under the title "echoic eavesdropping." The paper provides a range of citations, but without considering the large collection of engineering papers related to bistatic radars/sonars. Page 66 goes to considerable length to distinguish the dolphins potential for bistatic sonar operation as opposed to broader usages of the term echoic eavesdropping among other animal species. He reviews experiments where dolphins were challenged to interpret target information based on sonar signals emitted by a different dolphin (or facsimile thereof). A problem in many of these experiments was the limited recording bandwidth available in the man-made audio equipment of the specific eras. They note particularly the experiments of Xitco & Roitblat (1996) where the dolphins were kept near to each other and formed what is generally known as a pseudo-monostatic sonar system (transmitter and receiver near to each other relative to the distance to the target). The field patterns of the dolphin when transmitting and when receiving are highly relevant to the question of pseudo-monostatic versus bistatic sonar operation. In either mode, the successful interpretation of target information indicates the receiving dolphin was not making optimal use of the round trip time measurement capability associated with its intrinsic signaling system. They also noted the experiments of Gotz et al. (2005) that was restricted to pulse signals associated with free swimming dolphin pods where it appeared that one dolphin was echo ranging but others interpreted the target reflections as well. Their results indicated the pseudo-monostatic configuration was used by the dolphins with considerably better than chance performance.

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[154]Martin, S. et al & Houser, D. (2005) Instrumenting free-swimming dolphins echolocating in open water *JASA* vol 117(4), pt 1, pp 2301-2307

[155]Houser, D. & Martin, S. et al. (2005) Echolocation characteristics of free-swimming bottlenose dolphins during object detection and identification *JASA* vol 117(4), pt 1, pp 2308-2317

[156]Au, W. (2000) Echolocation in dolphins *In* Au, W. Popper, A. & Fay, R. *eds*. Op. Cit.pg 378

[157]Gregg, J. Dudzinski, K. & Smith, H. (2007) Do dolphins eavesdrop on the echolocation signals of conspecifics? *Intern J Compar Psychol* vol 20, pp 65-88

They also noted the experiments of Scronce & Johnson (1976) where the dolphins were clearly operating in the bistatic configuration. Their discussion is quite far-ranging and includes the potential for active jamming of each other if too many dolphins are echolocating monostatically at the same time while in close proximity to each other. In 2008, Gregg submitted this material as part of a dissertation that is also very useful along with a computer model for estimating the head angle and spatial distance of dolphins from underwater video footage[158]. The dissertation is very well structured but focuses more on behavioral aspects of echolocation than on the engineering aspects of the dolphins performance. In 2013, Gregg published a book for the popular audience on the intelligence of dolphins (and various ways of defining the term)[159].

### 1.5.3 The physical movements of dolphins during echolocation

Norris et al. (1990) provide a wealth of information concerning the physical protocol in their experiments and some specific information concerning the dolphin's movements in support of acoustic imaging of targets during echolocation[160]. They describe a rhythmic side to side head motion as well as a conical head motion. The latter is virtually identical to that used in man-made precision tracking radars.

## 1.6 The "fish stunning" performance of dolphins

Kassewitz has reported the first documented case of a dolphin intentionally stunning a fish (mullet)at a range of approximately two meters (private communications). They observed, videographed and recorded the acoustic actions of the animal. The acoustic signature of the attack is reproduced in **Figure 1.6.1-1**.

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[158]Gregg, J. Dudzinski, K. & Smith, H. V. (2008) 3D MASC: a method for estimating relative head angle and spatial distance of dolphins from underwater video footage. *Animal Behaviour* vol 75(3), pp 1181-1186.

[159]Gregg, J. (2013) Are Dolphins Really Smart?: The mammal behind the myth NY: Oxford Univ Press

[160]Norris, K. Howard, C. Marten, K. Wells, M. Wells, R. & Green, H. (1990) Collateral behaviors and rhythmic patterns In dolphin echolocation http://www.dtic.mil/dtic/tr/fulltext/u2/a246420.pdf

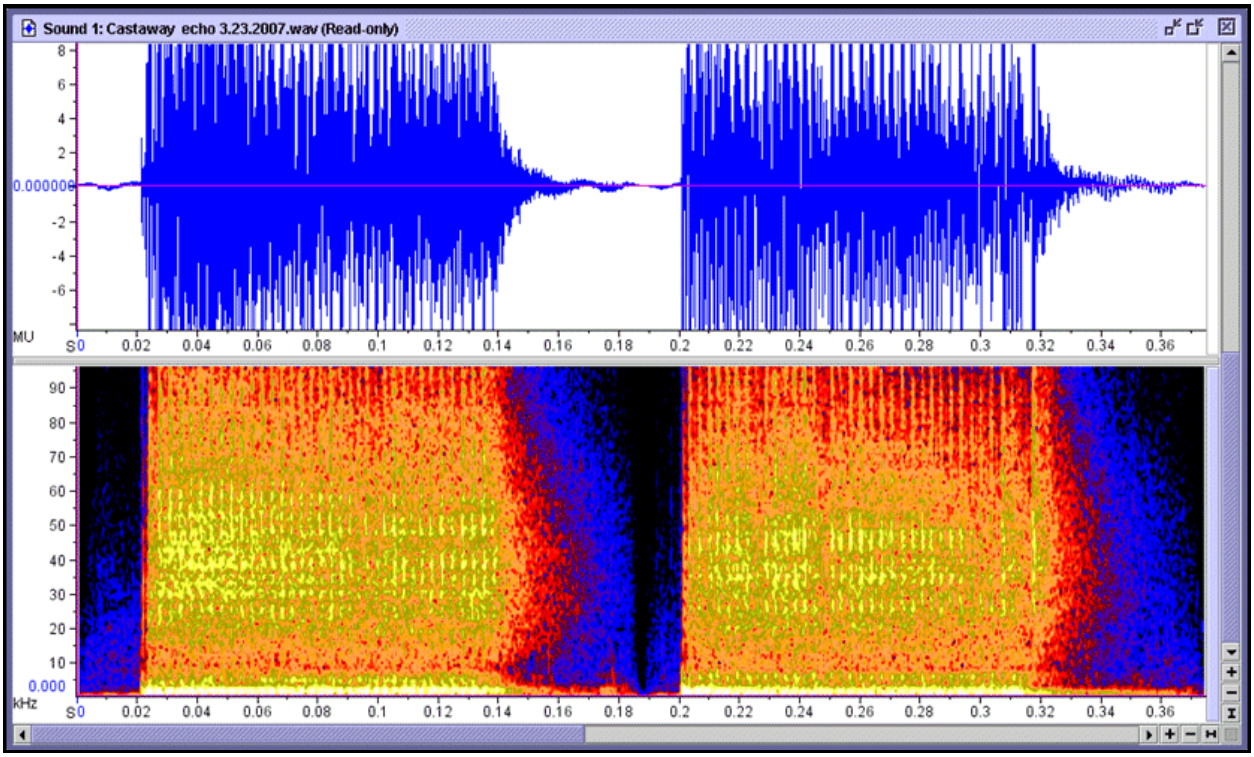


**Figure 1.6.1-1** Record of an acoustic stunning attack by a bottlenose dolphin. Two twelve millisecond bursts of mid frequency energy centered on 40 kHz. Upper frame shows relative power in MU versus time. Lower frame shows the energy quite widely distributed in frequency with a potential harmonic relationship with a fundamental of about 10 kHz. From Kassewitz, 2007.

The frequency spectrum of this 40 kHz waveform is somewhat unexpected since the beam forming mechanism available at frequencies in the 120-150 kHz region are not believed to be available in this lower frequency range. If true, the power density at a distance of two meters forward of the animal would be expected to be considerably lower than that achievable at higher frequencies for the same acoustic generator power. The two meter range is just beyond the estimated near-field radiation pattern of the 150 kHz beam forming mechanism. The nominal beam-forming gain for a ten-degree symmetrical beam is approximately 26 dB (412:1) over the isotropic condition.

**- - - - -END**

## 8.1.6.2 Potential range determination based on frequency dispersion

By employing surface acoustic wave technology applied to a liquid crystalline surface within the cochlea, frequency dispersion is avoided within the hearing system. However, frequency dispersion does occur in any Newtonian fluid forming the exterior medium, whether gaseous or liquid.

Frequency dispersion in the exterior environment can be used in hearing to estimate the range to a source. The effect is somewhat like the Doppler Effect. In the Doppler Effect, the pitch of a signal changes as a function of the velocity of the source. In this case, the individual frequency components

of an emitted sound travel through the medium at different phase velocities. This effect causes the envelope of the emitted sound to change with distance. It also causes the higher frequency components to reach a given point before the lower frequency components. If the auditory system is designed to detect the time of arrival of the individual frequency components of a well characterized signal, the system can estimate the range of the source. Lighthill develops the equations relevant to the dispersion of a bulk acoustic wave in a fluid but does not give practical values for the dispersion of sea water[161].

A potential exists for a whale to estimate the range to another whale emitting a standardized call through the frequency dispersion of the seawater. A brief literature search did not uncover dispersion data for very low frequency (well below 1000 Hz) acoustic dispersion in seawater.

[xxx calculate the phase delay or advance as a function frequency ]
[xxx must be a longitudinal wave in an unconstrained medium, deep water ]

[161]Lighthill, J. (1978) Waves in Fluids. NY: Cambridge Univ Press pp 235-245

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## Appendix L List of Figures 1/3/15

SUBJECT INDEX (using advanced indexing option)