Acoustics'08 Paris
June 29-July 4, 2008
www.acoustics08-paris.org

Investigation into the possible role of dolphins' teeth in sound reception

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Odontocetes use active sonar for echolocation, navigation and socialisation. This sonar is characterised by narrow transmission and reception directivity patterns, over a variety of ranges. There is physiological and behavioural evidence to suggest that dolphins hear the echoes of their high-frequency clicks through their lower jaws. Current theory suggests that sound is transmitted through a thin region at the base of the jaw into a waveguide leading to the ear. The angular precision predicted by this theory is however much less than dolphins have been observed behaviourally to be able to do. A novel hypothesis is that the teeth of the dolphin's lower jaw act as an end-fire sonar array. This paper will start by putting these competing hypotheses into their context, presenting bioacoustics in the ocean, dolphin echolocation physiology and acoustic behaviour, and presenting the mechanical properties of bones and teeth. This information is used to model the reception of different sounds by bottlenose dolphins (*Tursiops truncatus*) with each possible mechanism, investigating the variations with nerve delay, the role of the jaw relative to the teeth, and the resulting changes in frequency sensitivity and directivity. The results can then be compared with observations of behavioural patterns.

1 Introduction

Dolphins generate sound to communicate and localize objects underwater. The signals produced are transmitted into water and reflected from potential targets. Backscattered sound is then received by the dolphin, transmitted to the ear and processed. Many researchers have assumed that odontocetes receive sound waves solely through their lower jaw [1-6]. Sound enters the lower jaw, penetrates the thin pan bone of the rear mandible, is then conducted through the mandibular fat body and transmitted to the middle ear [2]. Observations of dolphins show however that the arrangement of the teeth is highly regular and might also play a role in sound reception (Fig.1). This was first suggested by [7], based on the specific arrangement of the teeth in the jaw, their regular spacing, the jaw geometry and the tooth nerve structure. They suggested that the teeth act as a passive resonant receiver, combined as two equispaced line arrays, with the nerves introducing progressive delays, as in a delay-line beamformer (Fig.2). [7] noted that the slow propagation of nerve impulses implied a progressive delayed response related to the position in the jaw and, since the tooth nerves proceed in parallel as part of the mandibular and then trigeminal nerve, that the signal arrival times at the pons (structure located at the brain stem) depend on individual nerve lengths.

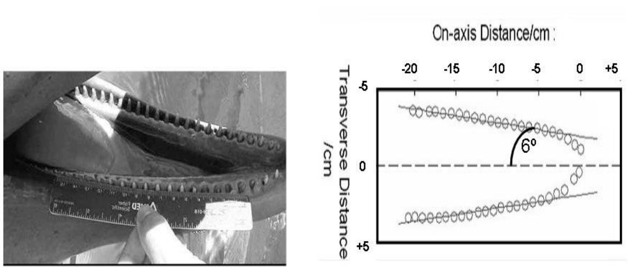

Fig.1: The dental arrangement for a bottlenose dolphin (*Tursiops truncatus*), as observed by [8] (left), modelled as a receiving array made of equally spaced teeth at a fixed angle (right, from [9]).

This topic was followed by [9, 10], who suggested that combining the rows of the teeth in a monopulse configuration would yield accurate angular resolution, with wide beams for rapid searching. [9] suggested that an echo arriving from a direction along the axis of the row of teeth (end-fire) would combine constructively before analysis by the central nervous system simultaneously (Fig.2). The present study aims at investigating the feasibility of both hypotheses (role of jaw/teeth in reception), either independently or in conjunction.

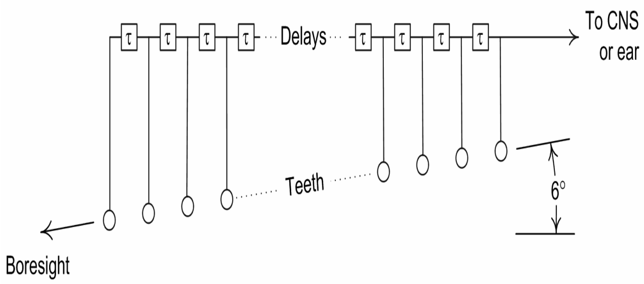

Fig.2: Each row of teeth can be considered as an end-fire array beamformer [11].

2 2-D Approach

Dolphin jaws have been modelled as simple arrays of hydrophones [8, 9, 11]: each tooth acts as an independent receiver and its signal is combined with others, with a suitable time delay depending on nerve length (Fig.3). Using the bottlenose dolphin (*Tursiops truncatus*) as an example, 44 hydrophones (22 on each side of the lower jaw) are set in a row, on average spaced 10 mm apart and at an angle of 12°. The whole construct is under water, and different types of signals are transmitted towards it. Observations of real, live dolphins show there are deviations of teeth positions from the ideal case (straight line, constant angle) and that end-fire configurations are only a limited subset of possible cases, especially if dolphins can use signals of opportunity (e.g. [13]).

As a first approach, we have constructed a 2-D model of the dolphins' teeth. Our model can account for small variations in teeth positions and sizes, and variable nerve delays. The effect of missing teeth can also be modelled. The time and frequency response of dolphins' jaws varies with the types of incoming signals (e.g. echolocation clicks, typically 100-135 kHz or communication whistles, typically below 50 kHz) and their angles of arrival in the plane of the jaw (Fig.3).

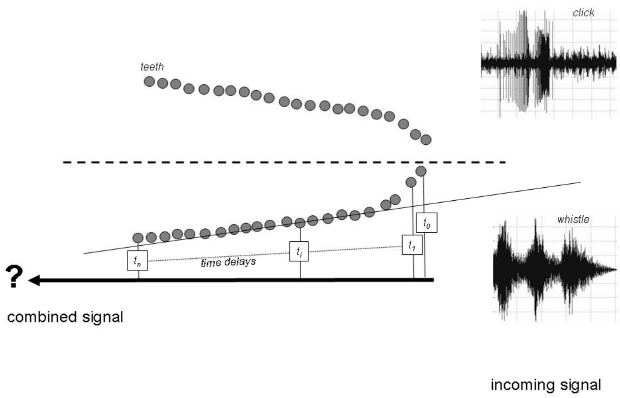

Fig.3: Individual teeth modelled as simple receivers. Incoming signals are combined after propagation with individual time delays corresponding to the nerves.

This model is based on the MATLAB implementation of a 2D pseudo-spectral, time domain solution of the acoustic wave equation [14]. It uses pseudo-spectral methods to calculate spatial derivatives and a staggered Adams-Bashforth method to integrate forward in time. A perfectly-matched boundary layer is applied at the edges of the calculation domain. This model can include nonlinear propagation and frequency dependent attenuation, although this was not used here. The sound pressure is calculated on each part of the calculation domain at a resolution of λ/8.

Dolphin teeth are not point receivers: their diameters vary with individuals and with their position (larger toward the back and smaller toward the front), and whether they are measured near the tip or at the bottom. Typical sizes vary between λ/2 and λ/4, depending on the signal's main frequency. Models have used both tip and bottom diameters from the cast of a dolphin's jaw. The speed of sound in teeth varies, but current measurements indicate transverse and longitudinal velocities of 2200 m/s and 3380 m/s respectively. The density of teeth used is the nominal value measured for a fully filled tooth of 2035.4 kg/m^3 [15]. The model has been run looking at different orientations of waves coming in the plane of the jaw.

Typical snapshots are shown in Fig.4 (in this case, for the tip of the teeth). There are clear areas of enhanced sound, moving away from the jaw. There are clear areas where the sound pressure is greatly reduced, their size extending toward the back of the jaw as the wave propagates. Teeth further away tend to be masked by teeth in the line of sight from the transmitter. Finally, there are clear indications of multiple scattering. Signals backscattering on teeth further back in the jaw create signals later in time on teeth already ensonified and, depending on teeth positions, it can be as high as 25% of the maximum level (Fig.5). These effects are exacerbated as teeth increase in diameter (e.g. when looking at the bottom of the teeth). They significantly modify the signals received by each tooth, showing that the teeth cannot be considered as isolated, point-like receivers. Furthermore, these effects are only modelled here in the horizontal plane. 3-D propagation is likely to enhance these effects, especially as the model is refined and other acoustic scatterers are considered (blubber, skin, actual jawbone, etc.).

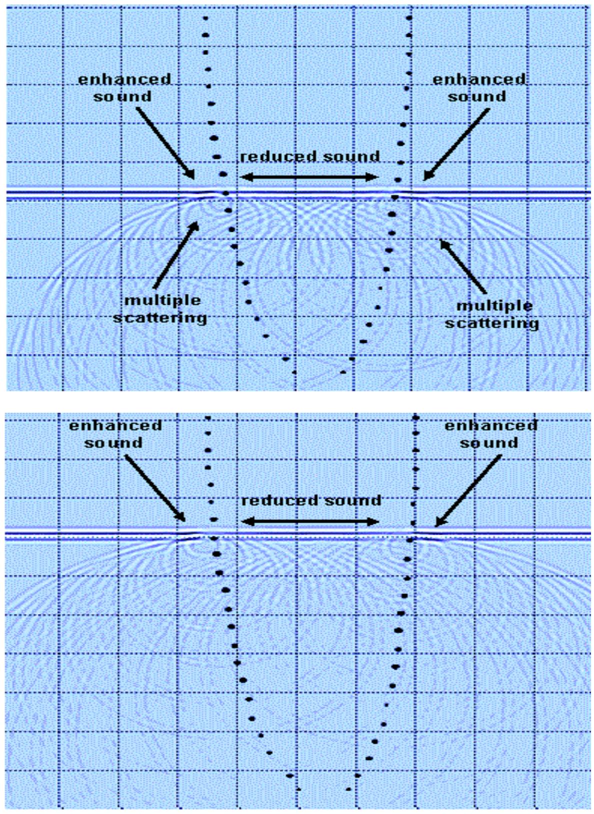

Fig.4: Teeth affect the propagation of a plane wave coming from the front of a dolphin. There are areas of reduced sound, increasing in size as the wave propagates toward the back teeth, areas of enhanced sound, and sometimes significant multiple scattering on the neighbouring teeth.

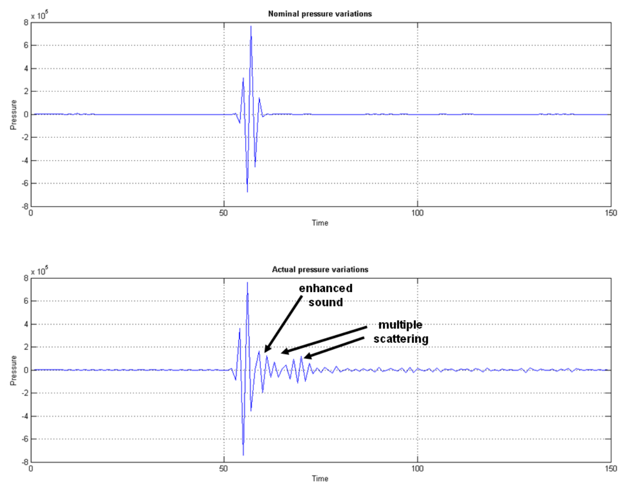

Fig.5: Top: signal expected at a tooth modelled as a point receiver. Bottom: signal actually received at the tooth, if modelling tooth size and position. Note the presence of enhanced sound immediately after reception of the original signal, and the high level of multiple scattering.

3 3-D Modelling

The construction of an accurate 3-D model of a dolphin's jaw is made possible by recent advances in measurements of the acoustically-related properties of its constituents (e.g. [12, 16-20]) and in understanding sound production in dolphins and whales [16]. Section 2 showed the importance of the exact position of each tooth, and of its diameter variations (e.g. from the tip to the bottom, where effects such as shadowing and multiple scattering will increase). Laser Doppler Vibrometry measurements of dolphins' teeth [12] have added to the knowledge of the modal structure of teeth, showing, for example, that they have strong resonances at 115-135 kHz. Inner variations in each tooth (e.g. density, tooth age) have to be related to their immediately surrounding environment.

The areas of enhanced scattering identified in Section 2 impinge on the skin each side of the jaw. It consists of three layers: the epidermis, dermis and hypodermis (blubber). The thickness of epidermis and dermis of six different areas was measured by [17]. The lowest measurement of the epidermis/dermis at the back of the dolphin was 0.17 cm, whereas the lowest thickness of the hypodermis was 1.54 cm. Since the skin around the dolphin's mouth is assumed to be thinner than at the rest of the body, this lowest value can be used. Current estimates of skin sound velocity are close to 1600 m/s [19]. It is also less dense, close to 969 kg/m^3 in average.

The tooth sockets are placed in gums, whose acoustic properties are currently assumed similar to that of skin, in the absence of any published measurements. The jaw bone is an important factor in the modelling. Its acoustic attenuation factor is very high (1.2 dB/mm according to [12]), leading some to conclude that the hard material of the jaw bone is not the primary pathway for sound reception, although recent measurements show there is some coupling [12]. Our model uses sound velocity for bones varying between 1900-3300 m/s [8] and bone densities around 1785 kg/m^3 [20], commensurate with other *in situ* measurements.

The nerves below the teeth are also part of our 3-D model. Although they are comparatively small, the low velocity of sound propagation along the nerves (100 m/s) [8] has clear influences on how and where appropriate acoustic signals are picked up and how they propagate (e.g. [7]).

These individual components can be combined in a 3-D model of the jaw and teeth with the different fatty tissues. The geometries are available from measurements of live and dead dolphins (e.g. [18]), and Figs. 6 and 7 show how they can be used together. Finite-Element modelling is currently underway, using ANSYS. As in Section 2, different types of incoming sound waves are used (varying frequency contents, like echolocation and communication vocalisations), but it is now possible to investigate out-of-plane directions, and the teeth are not considered as isolated acoustic scatterers, but as part of a whole.

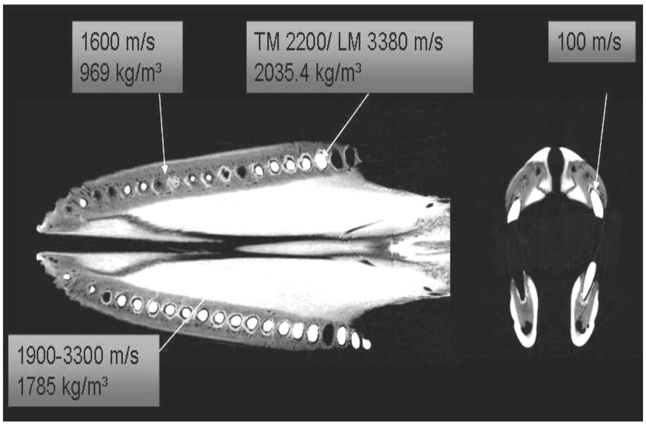

Fig.6: Sound velocity and density of skin, bones, teeth and tooth nerves. Sound velocity of the transverse (TM) and longitudinal mode (LM) were both included. On the left: top view of the lower jaw. Right: cross section of the lower jaw (from [18]).

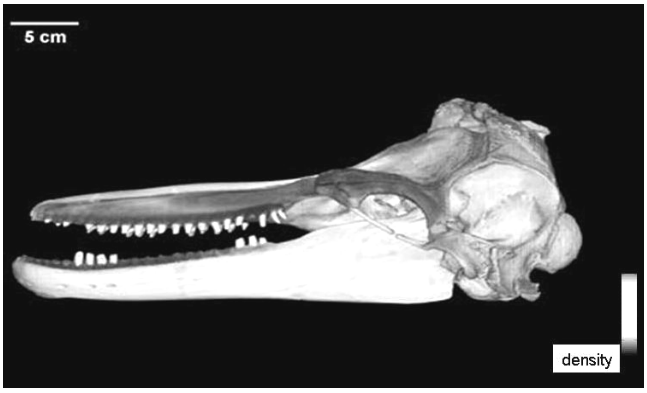

Fig.7: Lateral view of a dolphin's jaw (from [18]).

4 Discussion – Conclusion

The work presented here intended to look at two hypotheses for sound reception in dolphins (Section 1). The first assumes that odontocetes receive sound waves solely through their lower jaw [1-6]. Observations and preliminary models of teeth as beamformers have, however, suggested a second hypothesis; namely that teeth are the main source of sound reception [7, 9-11]. These two hypotheses need not be exclusive, and we have used measurements from the cast of a dolphin jaw to look at acoustic propagation within the jaw, and what types of signals are actually received by individual teeth.

The 2-D modelling of sound propagation within the jaw (Section 2) shows that sound levels can be enhanced, or reduced, and that there is significant multiple scattering for some teeth (Fig.4). The first implication is that teeth cannot be modelled as point-like receivers. Typical echolocation clicks last between 50-200 μs, with a broad frequency range of ~100-170 kHz depending on circumstances [7]. The mixing of secondary peaks (scattered from neighbouring teeth) with the signal currently received at a tooth (e.g. Fig.5) means that individual clicks might become undistinguishable at certain receivers. This has implications about how the signal from certain teeth is transmitted to the nervous system (e.g. nerve delays and/or attenuation of certain frequencies). As these models are very schematic, limited to waves in a plane (e.g. tip or bottom of the teeth), they cannot be used to assess other models such as those of [8, 9]. The different sections need to be considered together, adding the effects of the jawbone, blubber, skin etc., and this led to the design of 3-D models.

This was presented in Section 3. The design of an appropriate 3-D model has been made difficult by the dearth of actual measurements presented in open literature, sometimes conflicting and sometimes not fully explained. Several recent articles (e.g. [12, 16-20]) have however presented more authoritative, detailed measurements and analyses. These are now being used for Finite-Element investigations using ANSYS, and looking at the entire structure of the dolphin's jaw. These will be complemented with laboratory measurements using a hydrophone array, closely linked with observations of live dolphins.

Acknowledgments

This work corresponds to the first year of a postgraduate thesis and funding by a University of Bath Studentship is gratefully acknowledged. The authors would like to thank Peter F. Dobbins (SEA Ltd) and Paul A. Lepper (U. Loughborough) for the loan of a dolphin jaw cast and a hydrophone array.

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