Bio-Acoustics 2007

Proceedings of the

Institute of Acoustics

Fourth International Conference on Bio-Acoustics

Holywell Park, Loughborough University, 10-12 April 2007

Editors:

Simon Dible
Peter Dobbins
James Flint
Ed Harland
and
Paul Lepper

Bio-Acoustics 2007
Proceedings of the
Institute of Acoustics
Volume 29. Pt.3 2007

Edited by:
Simon Dible, Loughborough University
Peter Dobbins, Systems Engineer and Assessment Ltd
James Flint, Loughborough University
Ed Harland, Chickerell Bioacoustics
Paul Lepper, Loughborough University

Institute of Acoustics
77A St Peter's Street
St Albans
Hertfordshire
AL1 3BN
UK

ISBN 1 901656 85 3
ISSN 1478-6095

Printed by
The Printing Unit
University of Bath

FOREWORD

In December 1997 the first Institute of Acoustics Symposium on Underwater Bio-Sonar and Bioacoustic Systems, inspired largely by the enthusiasm of the late Dave Goodson, brought together underwater bio-acousticians and sonar engineers from around the world to look at a variety of acoustic topics relating to marine mammal sonar systems, the process of environmental impact assessment and the development of specialised tools. The 2nd Symposium in 2001 continued the theme, but extended area of interest to encourage contributions relating to fish.

In 2004, the area of interest was further extended and taken out of the water and into the air to include bats. This proved to be highly successful and demonstrated that, even within the general field of bioacoustics, there are areas of specialism that might benefit from a greater degree of communication and interaction.

In this conference we have taken this to the limit, and aimed at encouraging contributions relating to "all living things" and we have certainly been successful in covering a wide range of subjects and the keynote speakers will deal with:

- Using time synchronized low power autonomous recorders for marine mammal acoustic localisation (AB Wood Lecture)
- Adaptive and evolutionary aspects of call design in echolocating bats
- Detection and discrimination of complex sounds by birds in quiet and noise
- Pulses, patterns paths: sound processing in the cricket auditory system
- Current research trends in cetacean bioacoustics

Besides these, we have papers on fish, crustacean and land mammals as well covering topics such as the environmental impact of anthropogenic noise.

Clearly, bioacoustics is a wide-ranging interdisciplinary science. In many ways this is a good thing and we hope that one of the benefits of an event like this is that those who, for example, work with whales and dolphins underwater might learn something from those who study bats or birds, and vice-versa.

Finally, we wish to thank all the contributors for providing such a wide range of interesting and innovative material and especially acknowledge the help of the referees while preparing the manuscripts. Special thanks are also due to Simon Dible for setting up the web site and keeping the abstract and manuscript submissions under control.

Peter Dobbins
Systems Engineering & Assessment Ltd.
April 2007

CONTENTS

Page

POSTERS

MECHANISMS OF A DOLPHIN'S ECHOLOCATION HEARING.

VA Ryabov Karadag Natural Reserve NAS of Ukraine, Feodosiya, Crimea, Ukraine.

1 INTRODUCTION

Although the study of Odontoceti's hearing have received considerable attention in recent years, there is no understanding of how sound to animal's inner ear is transmitted and two pathways are considered in the main. The first pathway is the external auditory meatus and the middle ear [1-3], although there is mind that external auditory meatus generally does not participate in the sound transmitting to the middle ear [4-6] or it is used for transmitting of low frequencies [7, 8, 9]. Be based on the sound transmission through external auditory meatus, the subsystems existence possibility of passive hearing (1-10 kHz) and of active hearing (about 100 kHz) are discussed [10]. The second pathway includes the lower jaw fat body and the tympanic bone excluding external auditory meatus and tympanic ligament [5, 8, 11-13]. The returning echo apparently is transmitted into the fat body of lower jaw through mental foramens [11], or directly through the lower jaw bone in area of an "acoustic window" [12]. The fat body as medium and waveguide transmits returning echo onto lateral wall of tympanic bone playing here a role of the tympanic membrane [11-16]. Acoustical shielding of the lower jaw makes difficult the performance of echolocation tasks by dolphins [17]. Dolphins utilize frequency band of 40-140 kHz for discrimination of targets by echolocation what is considered as the frequency band of both sonar and echolocation hearing [18, 19]. It has been shown that acoustical stimulation of the lower jaw provokes considerable evoked potentials in central auditory system of dolphins [5, 8]. However regions with maximum sensitivity of the lower jaw surface to stimulation by the point sources of sound (size smaller than wavelength) [5, 8, 20-22] are different, and the results do not explain mechanisms of sound transmission. Along with this, the possibility of simultaneous participation of both external auditory meatus and an "acoustic window" for passing sounds to cochlea, when forming of space auditory image by dolphin [23], also is discussed.

Data of overview indicates that dolphin's lower jaw participates in perception of returning echo. Hence, it does apparently can be considered as the peripheral part of echolocation hearing. At the same time It Is not clear: (i) by what pathway the returning echo passes into the fat body; (ii) what morphological structures forms directivity of echolocation hearing; (iii) what mechanisms provide high accuracy of sound source localization. Along with this, results of echolocation tasks modeling [24-26] give a good reason to consider the mental foramens as canals for echo transmission into the lower jaw fat body. In this case, every half of lower jaw is considered as the traveling wave antenna (TWA) [26-29], and its morphological structures are considered as components of the peripheral part of echolocation hearing. The lower jaw is filled with fat body and neurovascular bundle [12,14, 30]. The acoustic impedance of these tissues is close to the impedance of sea water [31], hence they do not introduce of acoustic heterogeneities. Walls of both mental foramens (MF) and mandibular canal (MC) are acoustically elastic. Consequently, the sound conduction via MFs and MC can be analyzed on the basis of canals geometry. The objective of the study is the investigation of echo-transmitting mechanisms of the specialized peripheral part of echolocation hearing. Some particular objectives of the study are the investigation of the mandible morphology; measurement, analysis and simulation of the morphological structures under study, using the acoustic concepts and relationships.

2. MATERIALS AND METHODS

Bones of the lower jaw and the skull of an adult dolphin (Tursiops truncatus) were used for the study. The mandible was sawed in the MFs region to study morphology and to perform measurements. Hereinafter, they are indicated in the text as MFn, where n is the number of canal, counting from the tip of rostrum; n = 1, 2, 3, 4 (Figure 1). The cross sections dimensions of MFs were measured by plastic wedge with graduated width. Two measurements were realized for every foramen, first - for maximal transverse dimension of MF and next - in mutually perpendicular plane. The acoustical horn parameters, for every half of the lower jaw, were computed with using the catenoidal horn model. From the theory of acoustical horn it is following that the efficient transfer of acoustic energy by the horn is possible only on frequencies $f \geq 2.3f_c$, where f_c is the cut-off frequency. In this case the horn radiation resistance is reaches 0.9 maximum and the reflection from its mouth becomes insignificant. Whereas for frequencies below f_c radiation resistance tends to 0 and the radiation impedance becomes reactive. The cut-off frequency (f_c) is the lowest frequency at which the horn transmits the acoustic power [39], it is defined as, $(C_m / \lambda_c) \geq 1$; where C_m is the circumference of the mouth of the horn; λ_c is the cut-off wavelength. Practically it is choosing

$$C_m = \lambda_c , \quad n \quad f_c = c_0 / \lambda_c \quad \text{where } c_0 \text{ is the speed of sound} \tag{1}$$

The cut-off frequency of catenoidal horn also depends from the horn's flare rate [32], as

$$f_{c\xi}=(c_0\xi)/(2\pi), \tag{2}$$

where c_0 is the lower jaw fat body sound speed (1500 m/s); ξ is the horn flare constant, it appears in the basic catenoidal horn formula,

$$S_x=S_0(\cosh(\xi x))^2, \tag{3}$$

where S_o is the area of the horn throat; S_x is the area at distance x from throat
Sound pressure amplitudes of passed reflected and incident waves, in the acoustically narrow tube with cross-section jump may be expressed as [33],

$$A_2 = (2\sigma_1/(\sigma_1+\sigma_2))A_1; \tag{4}$$

$$B_1 = ((\sigma_1-\sigma_2)/(\sigma_1+\sigma_2))A_1, \tag{5}$$

where, A_2, B_1 and A_1 are sound pressure amplitudes of passed, reflected and incident waves, respectively; σ_1 and σ_2 are the cross-sections areas of neighbor pats of tube.

3. RESALTS AND DISCUSSION

The photographs of the mandible and the skull which were used in the study are shown in Figures 1-3. Prima facie, the mandible seems very simple because it represents two rectilinear hollow bones connected in the nasal part along the midline by an interlayer of cartilaginous tissue which is ossified (synostosizes) with age. In nasal part of the lower jaw on every its side there is the row of MFs. The angle between mandible bones in the MFs region is about 17°, increasing to about 30° posteriorly. The length of base on which MFs are situated is 81mm on the left and 87 mm on the right, and ones are considered as the bases of respective antennae of traveling wave (TWAs) [26-29]. The slope angle of lateral walis (in cross-section plane) relatively to medial plane is about 30° in region of MF1 and MF2, and smoothly decreases to about 25° in the region of MF3. MFs are situated on different levels of walls (dorsal-ventral). Hence the angle between left and right bases is greater than the angle between bones and it is about 24°. The distance between MF1 of left and right halves of the mandible amount to 7.5 mm and is discussed as the base of echolocation hearing [26-29]. Let the longitudinal axis of dolphin coincides with a mouth line, in the medial plane (Figure 3). In this case the bases of MFs (i.e. of TWAs) are directed nasally and slightly dorsal under the angle of about 8°. The cross-section dimensions of MF1, MF2 and MF3 are smoothly increased to the MC in different degree up to 54%, except of MF4,

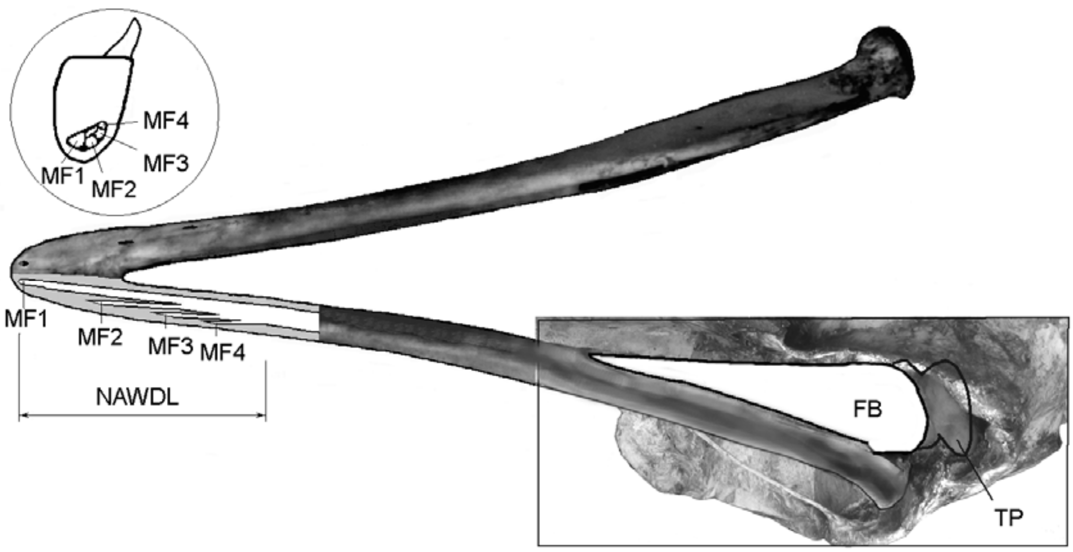


Figure 1 Ventral view of the mandible. The pattern of MFs position is shown in the nasal part section of mandible. The location of MFs within MC is shown separately in the circle, view in the nasal direction of the MC section, near the inner foramen - MF4, (magnified and turned around). The peribullar region is shown in the rectangle, ventral view. TP is the tympanoperiotic complex. FB is the mandible fat body.

(Table). The MFs cross-sections total area on external side of lower jaw (Figure 2A) is 18.04 mm^2 and 17.23 mm^2 on the right and on the left, respectively, and ones are discussed as the aperture of echolocation hearing. The shapes of MFs cross-section are oval. The MC is the prolongation of MFs (Figures 1, 3). The MFs are directed at the angle about 6°-10° (nasal and slightly dorsal) and at the angle about - 8° - 0* (nasal and slightly lateral; where "-" the direction to adjacent mandible half denotes). In view of pronounced anterior MFs directivity on Figure 2A ones look like almost round ovals whereas on Figure 2B they look like elongated ovals. The external aspect of the mandible is characterized by an oblique MFs section (Figure 2B). The walls of MFs and MC are consisting of dense bone. The cross-section area of MFs and the distances between them decrease with the distance from the tip of rostrum. All MFs differ in the length, in the cross-section size and in the length of oblique end, (Table). In MFs region, after every MF penetration into MC (Figure 1), the MC width (laterally)

A

B

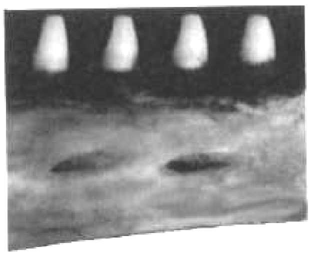


Figure 2. (A) The dolphin skull front view shows MFs of the lower jaw, four on the right, and three on the left. (B) The fragment of right half of lower jaw shows the typical form of the MFs oblique end from the outside of lower jaw, lateral view of MF3 and MF4.

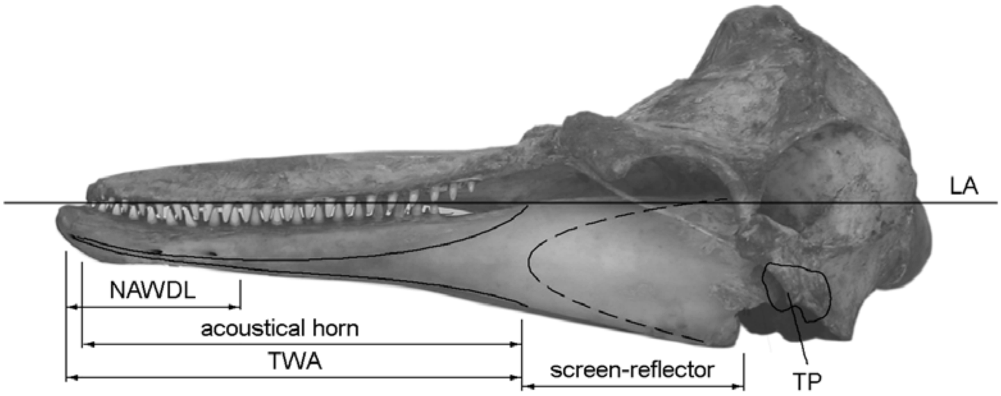


Figure 3. The dolphin skull, lateral view, left side. LA is the animal's longitudinal axis. The profile of MF1 and MC is indicated by solid line. The lower jaw region with MFs and anterior part of MC is the nonequidistant array of waveguide delay lines (NAWDL), about 100 mm in length. The acoustical horn is part of MC from internal orifice of MF1 to screen-reflector region, about 246.5 mm in length. The horn throat of oval shape has dimensions about 3.3 x 3.5 mm and the cross-section area about 9 mm^2. The horn has a flat mouth with cross-section area of about 492 mm^2; the shape of its section is elongated ellipse with axes dimensions of 2a=15 mm and 2b=44 mm. The traveling wave antenna (TWA) represents the complex of NAWDL and acoustic horn. The acoustically opaque screen-reflector is the lateral wall of posterior end of the lower jaw, from horn mouth up to the joint, about 132 mm in length (nasal-caudal), its dorsal-ventral dimensions are 55 mm and 88 mm near the horn mouth and near the joint, respectively. TP is the tympanoperiotic complex.

increases from 3.3 mm near MF1 to 7.5 mm near MF4. The MC dimensions (dorso-ventral) in this region increase in lesser degree from 3.5 mm near MF1 to 4.5 mm near MF4. The flare rate of the MC (caudal) increases both laterally and dorso-ventral (Figures 3, 4). In whole, the MC width (laterally) increases from 3.3 mm near MF1 (at horn throat) up to about 15 mm at external foramen of MC (at horn mouth), Figures 1, 3. The MC height (dorso-ventral) increases in greater degree from 3.5 mm near MF1 to about 44 mm at external foramen of MC. The MC cross-section shape near MF1 is close to oval, near MF4 it is close to semicircle. The shape of MC external foramen is close to elongated ellipse. The MC cross section area smoothly increases close by catenoidal law (R = 0.993), Figure 4. The approximation is more correct if we approximate by the cone in area of MFs and further - by the catenoid, then, R^2 = 0.996. In terms of acoustics, MC is an acoustic horn [26 29]. The left half of mandible has the similar structure, but only it has three MFs (Figure 3, Table)

The mechanisms of sound conduction of every peripheral receiver (TWA) are evident in a general way from Figures 1, 3. Incident sound wave (upon the lower jaw) stimulates the forced oscillations in MFs tissues, which are emitted into MC (into horn throat) and ones propagate farther by the fat body up to the tympanic bone (middle ear). Let's discuss it in detail. Both the MFs and the MC in terms of acoustic represent waveguides transmitting sound waves. It is known that only plane waves can transmit the signal without distortions in the waveguide [33]. Waveguides on frequencies below the first radial resonance or in other words the narrow waveguides (tubes) are practically used for this purpose, since ones transmit only the plane wave in axial direction. The cross-section shape of waveguide has little significance. For example, the waveguide of rectangular cross-section with the side A is narrow if $A < 0.5\ \lambda$; the circular waveguide of the radius R is narrow if $R < 0.61\ \lambda$. where λ is the wavelength. The dolphin sonar returning echoes which propagate through the MFs and MC are wideband (about 100 kHz) with energy maximum of about 110 kHz and the wavelength $\lambda_{110} \approx 13.6$ mm [18, 24], Therefore both the MFs (with cross section radius R < 1.6 mm) and MC in region of MFs (with radius R < 3.75 mm) represent narrow tubes in all frequency band of echolocation hearing about 40-140 kHz. For TWA operation it is necessary that there was the traveling wave regime in MFs and MC

MF number	MF length (mm)	MF transverse dimensions (mm)	MF cross section area (mm^2)	Distance to neighbor MF (mm)	MF fundamental tone (kHz)	Length of oblique end of MF (mm)
1						
left	10	3.2x3.2	8.04; 8.5	50.2	75	7
right	11	3.2x2.9	7.28; 8	36.1	68.2	8
2						
left	27.5	2.9x2.2	5; 7,7	31.2	27.3	11
right	35	2.6x2.1	4.29; 6.04	31.5	21.5	13.5
3						
left	12	2.9x2.2	5; 5,7		62.7	11
right	20	2.5x2.1	4.12; 4.94	19.15	37.5	11.5
4						
right	10.5	1.5x1.3	1.53; 1.53		71.5	10

Table 1. Basic characteristics of MFs. First and second numbers in column "MF cross-section area" are values from external and internal sides of MC, respectively. The length and the fundamental tone of MFs are indicated without taking of the oblique end into account.

and there were no their own resonance oscillations. The model of the narrow lossy tube with soft end caps and oblique end was used for analysis of sound conduction in MFs. In this case, it is possible to assume, that the losses will be caused by the tissues and nerves fibers. If forced oscillations are transmitted in the narrow tube then it is possible to neglect by natural oscillations because ones quick damp in the presence of losses [37]. The friction does not influence on forced oscillations except resonance cases. The natural oscillations frequencies (f_0) for narrow tube with soft end caps are determined as, $kL = l\pi$; where $k = (2\pi f_0)/c_0$ is the wavenumber; l =1, 2, 3, ..., is the oscillation number; c_0 is the sound velocity; L is the tube length; $f_0 = (lc_0)/(2L)$; The losses or damping decrement (η) which are necessary for exception of resonances possible be determined from known relations. A -3dB half-width of the resonant curve of natural oscillations corresponds to value variation of kL on ± ηkL i.e. relative frequency variation $\Delta f/f_0 = \pm\eta$; where Δf is frequency variation relative natural frequency of tube f_0; + and - correspond to values of η for frequencies above and below natural frequencies of tube. Hence Q-factor of

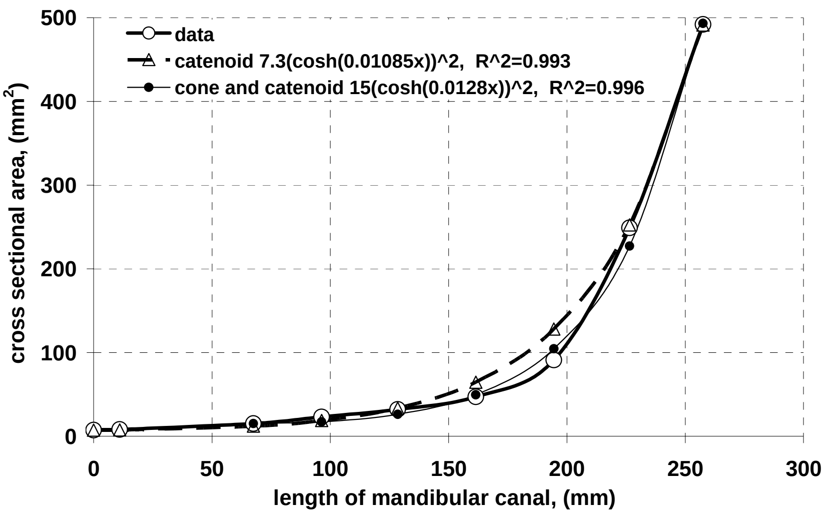


Figure 4. The dependence of cross-section area of the mandibular canal (horn) of its length (length of MF1+ length of MC, right half of lower jaw).

oscillations corresponds to Q=1/2η. When Q-factor of MFs is close to 1 then η=0.5 and the lower frequency of forced oscillations transmitting by MFs does not exceed 35 kHz (from computed values of natural frequencies, Table), higher frequencies are transmitted by overtones of MFs. Thus for getting of resonance characteristic of MFs within levels of -3dB in all band of echolocation hearing of 40-140 kHz (2Δf = 100 kHz) it is enough η = 0.5. In this case the transition time of forced oscillations in MFs for frequencies band of 2Δf = 100 kHz is 1/(2Δf) = 10 mks, and returning echoes transmission are realized without distortions even if their durations are about 30 mks. Moreover calculated transition time is matched with the potential time resolution of both the dolphin's clicks and echolocation hearing that are close to about 12 mks [18, 38].

It is known that the set of natural frequencies of narrow tube depends of the shape of its ending. Values of the end corrections were measured [33], they show variation of acoustical length of ending Δℓ in dependence of ratio d/λ; where d is the length of ending; λ is the sound wavelength; ℓ is the tube length. The ratio d/λ for MFs varies from 0.58 to 0.82, including the area of maximal steepness of variations. The values of Δℓ on frequencies 40-140 kHz for MFs vary from 4 to 9 mm. In comparison with tube possessing the harmonic set of natural frequencies, overtones of tube with ending are disposed non-harmonically, hence they are excited weaker and after discontinuation of forced oscillations damp faster. Therefore the oblique ends of MFs improve the damping of natural oscillations and therefore ones smooth the resonances characteristic irregularity.

Inside MC every of MFs openings represent the audio radiator (monopole) which returning echo radiates into MC. The undular dimensions of the radiator in frequency band of echolocation hearing amount to (kr = 0.12 - 0.94); where k = (2π)/λ is the wave number; r is the radius of MFs (0.7-1.6 mm); λ is the wavelength. On the frequency of the dolphin's sonar energy maximum (110 kHz), the undular dimensions of radiator amount to (kr = 0.67 or 2r/λ =0.23<1/3). Such radiator can be approximated by the pulsating small sphere with equivalent area [33]. It is known that radiation of the sound energy is proportional to the radiation resistance r_R of the radiator. For the pulsating small sphere r_R steeply increases with increasing of (kr) up to 0.5, as the square of frequency, further the growth speed of r_R drops and reaches 0.8 of maximal value, when kr=2. Therefore MFs as radiators have optimal undular dimensions and cross-section areas. What is the effectiveness of these radiators? The monopole radiates power in $1/(kr)^2$ less than a flat piston with the same area and particle velocity [37]. In our case, on frequencies of dolphin's clicks energy maximum the radiated power by monopole is less only in $1/(0.67)^2$ = 2.2 times, than it radiated by flat piston. Hence internal openings of MFs are very effective radiators, for given cross-sections areas.

The cross-section area of MC in the region of MFs increases relatively gradually. Here the MC height (dorso-ventrally) reaches of 4-4.5 mm, whereas its width increases, reaches of 7.5 mm. In region, where MFs penetrates into MC the cross-section area of every MF is essentially less than respective cross-sections of MC. Therefore when the returning echo passes through the discontinuity it is partially reflecting, in accordance with (4, 5). It is interesting that the reflection coefficient proportional to sections difference (σ_{MF}-σ_{MC}), i.e. the reflection is essentially less than the ratio of sections σ_{MF}/σ_{MC} [33]. Where: σ_{MF} and σ_{MC} are the cross-sections areas of MF and MC respectively. Hence only small part of energy is reflected by discontinuity. The calculations have shown that into MC more than 60% of echo energy passes even through MF3, where ratio of sections σ_{MF}/σ_{MC} amount to nearly 1/5. The apertures sections of MFs and ratio of sections σ_{MF}/σ_{MC} are decrease along the bases of TWAs (Table). Both of these factors set the falling amplitude distribution of receivers' array particles velocities of TWA [26]. Along with this, the time delays of sound arriving in MC depend both of the distance between MFs and of the angle of incident wave upon MFs (this dependence was considered at calculations of TWA beam pattern [26]). If the sound velocities in tissues of MFs differ from ones in tissues of MC then the MFs length will define the additional delay of sound arriving in MC independently of incident sound wave angle. Therefore MFs represents the nonequidistant array of waveguide delay lines (NAWDL) and they set phase distribution of TWA particles velocities. In the accessible references it was not possible to find data of a sound speed (C_{MF}) in tissues of MFs. At the same time modeling of the influence of C_{MF} for the shape of beam pattern gives grounds to suppose that optimal C_{MF} smoothes the irregularity of beam pattern [26]. It is interesting that MFs realize several the unite composite functions though paradoxical laconicism of morphology, at that, their dimensions are optimal for transmitting echo from the medium into the MC fat body, that confirm one of Norris suppositions [11].

The lower jaw's horn parameters were calculated by the model of the catenoidal horn, Figure 4 (approximation by the cone and catenoid). The cut-off frequency and the lower frequency limit were calculated from the equation (1), as f_c = 19.1 kHz, from here, the lower frequency limit defined by horn mouth dimensions, f = 19.1*2.3 = 43.8 kHz; from equations (1-3) are obtained, ξ = 0.01085; $f_{c\xi}$ = 2.58 kHz; and the lower frequency limit defined by horn flaring, f_ξ = 2.58*2.3 = 5.92 kHz. It is interesting that the catenoidal horn represent the variant of exponential hyperbolic horns and for given cut-off frequency it represent the most short horn from this family, i.e. it have maximal speed of section flaring. What functions the horn fulfills? The incident soundwave upon lower jaw pass into MC (horn throat) through the MFs. Therefore the horn throat plays a role of the summator of signals where echo signals of all MFs are being summed with respective amplitudes and time delays. Further the horn radiates their to the tympanic bone (middle ear) which is disposed close to the lower jaw joint. Odontocety possess the fat body which fills MC cavity and reaches tympanic bone. Tissues of the fat body are composed of unusual endogenously synthesized lipids and they are discussed as the medium for transmitting of sound into the region of tympanic bone where its wall is thinned up to 0.3-0.4 mm and it plays a role of tympanic membrane transmitting sound oscillations to the malleus of the middle ear [12, 14, 15, 16]. Therefore, the under consideration pathway of transmitting the returning echo into tympanic bone (excluding external auditory meatus) evidences that the lower jaw morphology structures presents component parts of the specialized peripheral part of echolocation hearing. The consecution of morphological structures which in terms of acoustics represents the optimal consecution of acoustic systems (Figure 1, 3) evidences the same.

The horn mouth effectively radiates only frequencies higher than f = 43.8 kHz, it is follow from calculations (see above). This result is of interest as defines the lower frequency limit of both horn and TWA and echolocation hearing as equal 43.8 kHz. Besides, it is consistent with the lower frequency limit of echolocation hearing (40-140 kHz) which has been measured in experiments of echolocation [18,19]. Hence, the horn plays a role of the high-pass filter because transmits to tympanic bone only the frequency of echolocation hearing and attenuates ones lower than 43.8 kHz. This fact indicates that the low-frequency sounds and communication whistles pass into the middle ear by another (low-frequency) pathway, this role apparently can play or the external auditory meatus [7], or the outer mandibular fats (external to the mandible but beneath the blabber) [14]. The low-frequency pathway evidently plays a role of the low-pass filter because it must transmit only the low-frequency sounds and whistles communications into the middle ear and must attenuate ones higher than about 30-40 kHz, that is consistent with [7, 8, 9]. The commonly used rule is that a horn must not handle frequencies higher than four octaves above its lower frequency limit, in order to ensure lower distortion levels [40]. The frequency band of the echolocation hearing of 40-140 kHz is less than two octaves; it is in agreement with the requirement to ensure lower distortion levels. The lower frequency limit calculated from the horn flare rate reaches f_ξ = 5.92 kHz, that somewhat below than lower frequency limit of echolocation hearing, nevertheless this is necessary for increasing the reproduction precision of signal [33]. The cross-section area of every MF smoothly increases along of MF. Hence, every MF and respective part of MC (from internal orifice of MF to the mouth of horn) together represents horn with the jump of cross-section. Although from the energy conservation law it is follow that the horn does not reinforce the echo energy, in the same time it is known that horn matches radiation resistances of the radiator (in horn throat) which possesses the dimensions in many times less than the wavelength with the wave resistance of the medium (in horn mouth). Hence, the MC horn matches the radiation resistances of radiators (internal orifices of MFs) with the wave resistance of fat body. Therefore the horn transmittes energy of returning echo sound wave from the medium to tympanic bone in all frequency band of echolocation hearing 40-140 kHz and excepts reflections and distortions. Without a horn only minor part of echo energy would reach the tympanic bone. On the other hand, it is known that the horn behaves as a transformer, converting acoustic energy at high pressure and low velocity at the throat to energy at low pressure and high velocity at the mouth [40]. In other words the horn amplifies the particles velocity and as a result, the MC horn obviously compensates the particles velocity amplification lack by the middle ear of Odontoceti, earlier revealed [16]. The sound source at the horn throat with flare angle (φ) radiates sound intensity in 4π/Ω more than pulsing sphere radiates into infinity [33]. Hence, it would be interesting to calculate the amplifying properties (K) of the mandible horn in comparison with an undirected source (monopole) as, $K = 4\pi/\Omega$, where: Ω is the solid angle, $\Omega = S/l_h^2$, where: S is the horn mouth area; l_h is the horn length. The effective horn length and therefore it's the gain constant decreases for MFs disposing further from tip of rostrum. The calculated intensity gain constants (K) of the mandible horn for right (left) half of the lower jaw through MF1 (MF1), MF2 (MF2), MF3 (MF3) and MF4 reach 2148 (2148), 466 (575), 201 (273) and 11 times, respectively, with consideration of external and internal orifices cross-section areas of MFs and MC. These gain constants were used as weight ratios for calculation of array amplitude distribution of TWA and beam pattern of echolocation hearing [29]. The horn supports traveling wave in MC, as reflections from a mouth to a throat (i.e. to NAWDL) are minor in all echolocation frequency band, as this follows from horn properties. This is a very important result as it defines the structure of an ideal Nature-created wideband TWA as complex composed by acoustic horn and NAWDL. This type of antennae is a version of group antennas. The maximum sensitivity of TWA coincides with the base directivity (direction of its greatest size) on which elementary receivers are located. In this case, TWA is more convenient compared with antennas with a maximum sensitivity situated perpendicularly to the base. Hence, it is clear that the MC of the mandible has been ideally utilized by Nature to design such an antenna.

At the posterior end of the lower jaw, the mandibular canal opens medially as the large mandibular foramen. The minimum thickness of the lateral mandibular wall (for Tursiops truncatus) in this region is about 1-3 mm [41], and Norris [12] proposed that the sound can pass into mandibular fat body through this wall as through the "acoustic window". Here in region of the large mandibular foramen (dotted line in Figure 3) the fat body goes out from mandibular canal and extend to the tympanic bone disposed closely to the joint. The undular dimensions (kL) of this region (the screen-reflector, Figure 3) amounts to kL> 25-40 (dorso-vental) and kL> 80 (nasal-caudal) on the frequency 110 kHz; where $k=2\pi/\lambda$ is the wavenumber, L is the typical dimensions of bones. Granting, that bones of the lower and upper jaw have large undular dimensions and acoustic impedance is more in 5 times of the water one, it is obvious that they play a role of effective acoustically opaque screen. When jaws are closed kL is about 100. For this screen the condition of geometrical scattering kL>>1 is completed, therefore for evaluation of the screen effectiveness the total internal reflection angle (α) must be take into account. The scull bones sound velocity amounts to c_b =3400 m/s [34], the water sound velocity take up equal c_0 = 1500 m/s, then, $\sin\alpha = c_0/c_b = 1500/3400 = 0.44$ and α = 26.2°. The width of the dolphin's sonar beam pattern in the horizontal plane is less than 10° relative to animal's longitudinal axis [35, 36], therefore, the angular domain of returning echoes is the same. Therefore, the returning echoes arrive to mandible's lateral walls (including the "acoustic window") in the angular domain of total internal reflection β ≤ 94° (Figure 5), and hence, the screening increases many times, therefore, this site can not be an "acoustic window".

The posterior end of the lower jaw is concave medially and convex laterally. Hence, there is a good reason to believe that this region presents also the reflector focusing the returning echo in frontal plane of the fat body and reflecting one to tympanic bone. The focusing of returning echo in sagittal plane is realized by the mandible horn which possesses the narrower beam pattern in this plane than in frontal one (it is evident from horn mouth dimensions in every plane). Therefore, MFs are the only pathway for returning echo to pass into mandible fat body. In this connection it needs to discuss the results of measurement of the surface sensitivity of the dolphin's head to the sound [5, 8, 20-22], All this measurements were realized with using hydrophones or jaw phones, i.e. by direct contact of the dotted radiators (dimensions are less than wavelength) with the surface of the head. Hence, the spherical wave is excited in acoustic near-field of dotted radiator (in head tissues and surrounding water) and therefore - in the region of the supposed reception primary site of returning echo. Unlike this the returning echo arrives to a dolphin's head from major distance. In this case the Fraunhofer field (an acoustic far-field) when phase difference between plane and spherical wave fronts is sufficiently small, begins from the distance (D) to non-directed sound source, which is defined as, $D \geq L^2/\lambda$, where: the receive aperture dimension, L ≈ 8 cm; λ is the wavelength (110 kHz) ≈ 1.36 cm; whence D ≥ 47 cm. Therefore, returning echo presents the

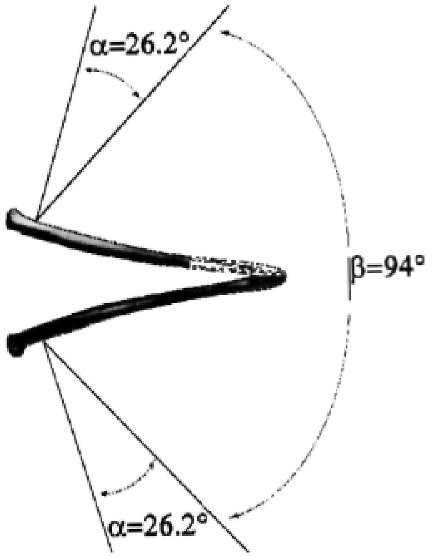


Figure 5. The lower jaw, ventral view. The critical angle of total reflection (α) for screen-reflector regions of left and right halves of lower jaw. The sector of the critical angles of total reflection of lower jaw, in frontal plane (β).

plane wave when arrives from distances more than 47 cm. The receiving aperture or array with dimensions more than the wavelength is destined to receive of the plane wave in acoustic far-field. As a result of this the spherical field of dotted source does not adequate to the receiver (i.e. TWA of the lower jaw) and this may be the cause that, in considered works, regions of maximal sensitivity are different and sensitivity maps are intricate. And in the main the authors did not explain the results of these activities uniquely and unfortunately these results do not elucidate the possible sound-conducting mechanism, and on the contrary they complicated of a model of a dolphin hearing. While the mandible conception as the system of two TWAs satisfactorily elucidates both the mechanisms of sound-conducting and formation of the beam pattern of entire peripheral part of echolocation hearing [26-29]. Moreover, the results of present work give good reasons to suppose that both left and right peripheral receivers of echolocation hearing consist from functional acoustic systems, conditional titles of which are shown in Figure 1, 3.

The results of this paper reveal that the peripheral part of echolocation hearing transmits the sounds only of echolocation frequencies band (40-140 kHz) into the middle ear while sounds of lower frequencies and whistles (up to 30-40 kHz) are transmitting by the other pathway. This fact supposes the existence of two hearing subsystems which differ by both frequencies bands and pathways of sound. Results obtained confirm the opinion about possible existence of the two auditory subsystems in dolphins [10], at the same time the results differ from this opinion at least by the frequency bands and sound pathways. The possibility of simultaneous participation both external auditory meatus and an "acoustic window" for sound conduction to cochlea [23] is impossible, from the point of view of results obtained.

It is known that a row of functional and morphological modifications occurred in cetaceans during the process of secondary adaptation to aquatic conditions of the environment. And the specialized peripheral part of echolocation hearing (which occupies the lower jaw very expediently), it seems belongs to theirs number. The results obtained give grounds to suppose the presence of similar peripheral part or echolocation hearing in Odontoceti.

REFERENCES

1. F.C. Fraser and P.E. Purves, 'Hearing in the cetaceans: Evolution of the accessory air sacs

and the structure and function of the outer and middle ear in recent cetaceans', Bull. Brit. Museum Nat.History, Zool. 7(1) 1-140. (1960).
2. F.V. Reysenbach de Haan, 'Hearing in whales', Acta otolaryngol. Suppl. 134 1-14. (1957).
3. W.H. Dudok van Heel, 'Sound and cetacean', Neth.J.Sea.Res.1 407-507. (1962).
4. M.Yamada, 'Contribution to the anatomy of the organ of hearing of whales', Sci. Rep. Whales.Res.inst. 8 1-79. (1953).
5. J.G. McCormick, E.G. Wever, J. Palin and S.H. Ridgway, 'Sound conduction in the dolphin ear', J.Acoust.Soc.Amer. 48, 6(2) 1418-1428. (1970).
6. G. Fleischer, 'Structural analysis of the tympanicum complex in the bottlenose dolphin (Tursiops truncatus)', J.Audit.Res. 13 178-190. (1973).
7. E.Sh. Airapetiantz, V.A. Voronov, U.V. Ivanenko, M.P. Ivanov, D.L. Ordovsky, V.V. Popov, B.F. Sergeev and V.I. Chilingiris, ‘To physiology of Black Sea dolphins's sonar', J.Evol.Bio. Physiol. 2 418-421. (1973).
8. T.H. Bullock, A.D. Grinell, E. Ikezono, K. Kameda, J. Katsuki, M. Nomota, O.Sato, N. Suga and K. Yanagisawa, 'Electrophysiological studies of central auditory mechanisms in cetaceans', Z.Vergl.Physiol. 59 117-156. (1968).
9. D.L. Renaud and A.N. Popper, 'Sound localization by the bottlenose porpoise Tursiops truncatus', J.exp.Biol. 63 569-585. (1975).
10. N.A. Dubrovsky. On the two auditory subsystems in dolphins: Sensory abilities of Cetaceans. Plenum Press, 233-254. (1990).
11. K.S. Norris. Some problems of echolocation in cetaceans: Marine bio-Acoustics, Pergamon press, 316-336. (1964).
12. K.S. Norris, The evolution of acoustic mechanisms in odontocete cetaceans: Evolution and Environment, Jail Univ. Press, 297-324. (1968).
13. K.S. Norris and G.W. Harvey, 'Sound transmission in the porpoise head', J.Acoust.Soc. Amer. 56(2) 659-664. (1974).
14. H.N. Koopman, S.M. Budge, D.R. Ketten and S.J. Iverson, ‘Topographical distribution of lipids inside the mandibular fat bodies of Odontocetes: Remarkable complexity and consistensy’, J.Ocean.Engin. 31(1) 95-106. (2006).
15. S. Nummela, T. Reuter, S. Hemila, P. Holmberg and P. Paukku, ‘The anatomy of the killer whale middle ear (Orcinus orca)', Hear.Res. 133(1-2) 61-70. (1999)
16. S. Hemila, S. Nummela and T. Reuter, 'A model of the odontocete middle ear', Hear. Res. 133 82-97. (1999).
17. R.L. Brill. The jaw-hearing dolphin: preliminary behavioral and acoustics evidence: Animal Sonar. Processes and performance, Plenum Press, 281-287. (1988).
18. V.A. Ryabov. Spectral-temporal analysis of acoustical pulse signals by a bottlenose dolphin. Candidate's Dissertation. S-Pb, (1991).
19. V.A. Ryabov and G.L Zaslavskyi, 'Noise immunity of Dolphin's sonar', Sensory Systems, 12(2) 202-209. (1998).
20. B. Mohl, W.W.L. Au, J. Pawloski and P.E. Nachtigall, 'Dolphin hearing: Relative sensitivity as a function of point of application of a contact sound source in the jaw and head region', J.Acoust.Soc.Amer, 105 3421-3424. (1999).
21. R.L. Brill, P.W.B. Moor and L.A. Dankiewicz, ' Assessment of dolphin (Tursiops truncatus) auditory sensitivity and hearing loss using jawphones', J.Acoust.Soc.Amer, 109 1717-1722. (2001).
22. R.L. Brill, P.W.B. Moore, D.A. Helweg and L.A Dankiewicz, 'Investigating the dolphin's peripheral hearing system: acoustic sensitivity about the head and lower jaw', Technical report, 1865 1-14. (2001).
23. L.K. Rimskaya-Korsakova and N.A. Dubrovsky, 'Two sound conduction pathways to the cochlea participate in formation of spatial auditory image in the dolphin', Sensory Systems, 12(4)497-506.(1998).
24. V.A. Ryabov and G.L. Zaslavskyi, Discrimination of targets at interfering reflections and monaural hearing of the bottlenose dolphin', Sensory Systems, 13(4) 337-344. (1999).
25. V.A. Ryabov. Evaluation of dimensions of the aperture and base for dolphin's echolocation hearing. <http://edok01 .tib.uni-hannover.de/edoks/e01 mr01/367010372.pdf> (2002).

26. V. A. Ryabov. Study of a dolphin lower jaw morphology and modeling of an echolocation hearing beam pattern. <http://edok01.tib.uni-hannover.de/edoks/e01mr01/367007592.pdf> (2003).
27. V. A. Ryabov Study of a dolphin lower jaw morphology and calculation of an echolocation hearing beam pattern. In Abstracts of the XIXth meeting of IBAC. < www.cultura.ufpa.br/ibac> (2003).
28. V. A. Rvabov 'A dolphin lower jaw is a hydroacoustic antenna of the traveling wave', In Abstracts of 146meeting of ASA, J.Acoust.Soc.Amer.114(4)2414-2415. (2003).
29. V. A. Ryabov, Lower jaw - peripheric part of the dolphin echolocation hearing, Proc. 3th Marine Mammais of the Holarctic, 483-489. Moscow (2004).
30. G.B. Agarkov, B.G. Khomenko and V.G. Khadzhinskyi. Morphology of dolphins, Naukova Dumka. (1974).
31. U. Varanasi and D.C. Malins, 'Unique lipids of the porpoise (Tursiops gilli): differences in triacyclglycerois and wax esters of acoustic (mandibular and melon) and blubber tissues, Biochimica et Biophysica Acta. 231 415-418. (1971).
32. Ya. Sh. Vahitov. Theoretical foundations of an electroacoustics and electroacoustical instrumentation, Iskusstvo. (1982).
33. E. Skudrzyk. The foundations of acoustics. Mir, (1976).
34. D. Giraud-Sauveur, Recherches biophysiques sur les osselets des Cetaces, Mammalia. 33(2) 409-431. (1969).
35. W.W.L. Au. Echolocation signals of Atlantic bottlenose dolphin (Tursiops truncatus) in open waters: Animal sonar systems, Plenum Press. 251-282. (1980).
36. W.W.L. Au. The sonar of dolphins, Springer-Verlag. (1993).
37. M.A. Isakovich. General acoustics, Nauka. (1973).
38. V.A. Ryabov and G.L. Zaslavskyi, 'Temporal analysis of returning echoes by dolphin, Reports of NAS of Ukraine. 2 188-192. (1999).
39. J. Dinsdale, 'Horn loudspeaker design', Wireless world. 3 19-24. (1974).
40. J. Dinsdale, 'Horn loudspeaker design', Wireless world. 5 133-138. (1974).
41. S. Nummela, J.E. Kosove and T.E. Lancaster, 'Lateral mandibular wall thickness in Tursiops truncatus: variation due to sex and age', Marine Mammal Science. 20(3) 491-497. (July 2004).

INDEX of AUTHORS **Page**

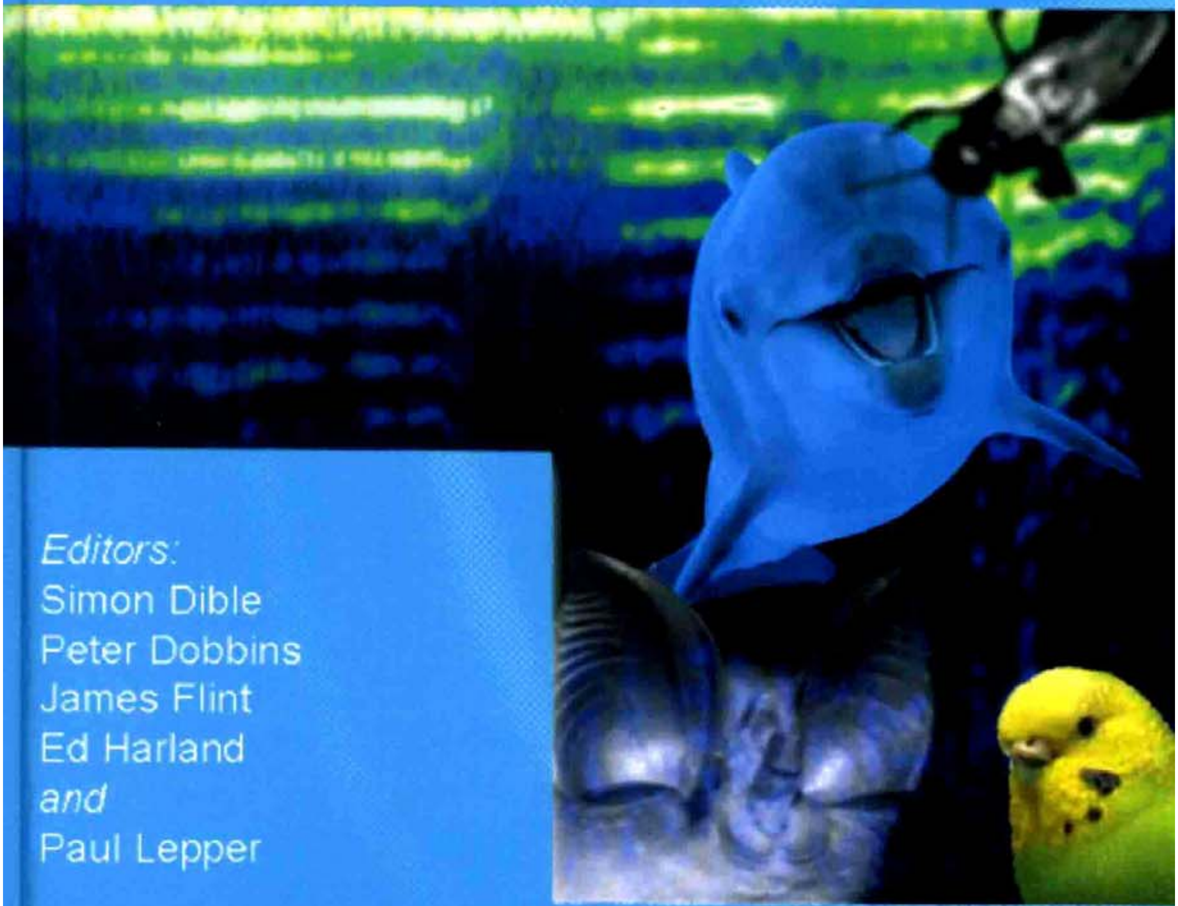
Bio-Acoustics 2007

Proceedings of the

Institute of Acoustics

Fourth International Conference on Bio-Acoustics

Holywell Park, Loughborough University, 10-12 April 2007



Editors:
Simon Dible
Peter Dobbins
James Flint
Ed Harland
and
Paul Lepper

S·E·A

[dstl]

Loughborough University

Chickerell BioAcoustics

Office of Naval Research GLOBAL Science & Technology

Institute of Acoustics