Dolphin hearing: Relative sensitivity as a function of point of application of a contact sound source in the jaw and head region

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(Received 20 April 1998; revised 16 February 1999; accepted 19 March 1999)

The auditory input area of the dolphin head was investigated in an unrestrained animal trained to beach itself and to accept noninvasive electroencephalograph (EEG) electrodes for the recording of the auditory brain-stem response (ABR). The stimulus was a synthetic dolphin click, transmitted from a piezo-electric transducer and coupled to the skin via a small volume of water. The results conform with earlier experiments on acute preparations that show best auditory sensitivity at the middle of the lower jaw. Minimum latency was found at the rear of the lower jaw. A shaded receiver configuration for the dolphin ear is proposed. © *1999 Acoustical Society of America.* [S0001-4966(99)05606-4]

PACS numbers: 43.64.Tk, 43.64.Ri [RDF]

INTRODUCTION

Dolphins are acoustically orienting mammals, adapted to the marine environment. Profound changes were required to transform an efficient ear for aerial sound, as present in the terrestrial ancestors of cetaceans, into one of equal or greater efficiency underwater. Mammalian soft tissues behave much like water acoustically. Consequently, underwater sound is not being reflected at the boundary of a body and is not easily channeled, as it is in, e.g., the auditory meatus of terrestrial mammals. In fact, a submerged mammalian body is quite transparent to sound (cf. ultrasonic scanning), with exceptions for volumes containing gas, or dense bone.

From anatomical observations, it is therefore difficult to identify a route of sound from the water medium to the inner ear in cetaceans. A variety of theories has been proposed, spanning from the completely sound-transparent head (Reysenbach de Haan, 1957), over meatal transmission (Purves, 1966) to the lower-jaw acoustic window and waveguide idea (Norris, 1964, 1980). Even hypotheses dispensing with the inner ear as the mechano-neuronal transducer have been proposed (Goodson and Klinowska, 1990).

Since the nature, shape, and size of the receiver are major determinants of the performance of any sonar, it is not surprising that a number of experiments have been designed to provide evidence of this matter. An early, classical paper by Bullock *et al.* (1968) used acoustically evoked potentials, recorded from the midbrain of a number of dolphins in acute preparations. Best sensitivity was found to sound applied to the front half of the lower jaw, in fair agreement with the jaw-hearing hypothesis of Norris (1964). Using cochlear microphonics in similar preparations, McCormick *et al.* (1970) obtained similar results. The jaw-hearing hypothesis was also supported by a psychophysical experiment by Brill *et al.* (1988). In this experiment, the target-detection ability of a trained dolphin, with and without sound-blocking material applied to the mandible, was found to be influenced by the blocking. Recently, Popov and Supin (1990) used a sound source in the far field and the auditory brain-stem response (ABR) with a time-delay, difference-based triangulation technique to determine the auditory input location of three dolphin species. This technique dispenses with surgical procedures, allowing physiological measurements from a lightly restrained, alert animal. They concluded that sound entered the ear in the meatal/bulla region and not via the mandible.

From knowledge on the directionality of the dolphin ear (Au and Moore, 1984) it can be inferred that the effective area of sound collection, the equivalent of the pinna of terrestrial mammals, is about 8 cm^2. The theories of the fully transparent head, and the meatal route, both appear inconsistent with this result. However, as the effective area consists of the sum of areas shaded in an unknown way, the directional evidence is not suitable for testing the theories.

Thus, the interpretation of the various experiments is not consistent, and even contradictory (Norris, 1964; Popov and Supin, 1990). Different approaches ranging from measurements on cadavers, over acute, sedated preparations, mildly restrained alert animals, and to fully cooperating, trained animals have been used. Some experiments were performed in air, others with submerged animals, some with far-field stimulation, others with point or contact stimulation. These varied approaches simply do not produce readily comparable results. The auditory input area in dolphins thus continues to be incompletely defined.

The approach of this work was to use a new combination of the above approaches. Stimuli were applied by a contact hydrophone in a suction cup to a female dolphin (*Tursiops truncatus*) trained to beach itself on a mat and remain motionless for minutes. Employing noninvasive electrodes, the ABR technique was used to quantify the response. The aim was to define the zone of entrance for sound by combin-

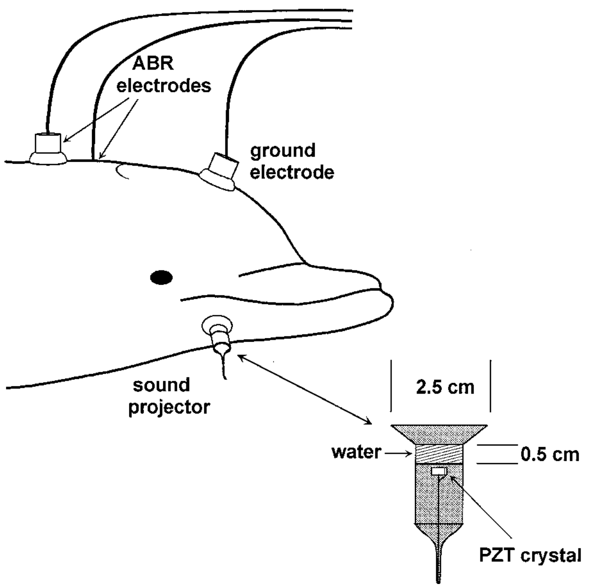

FIG. 1. Sketch of recording geometry electrodes, and of the sound projector.

ing knowledge of place-of-point stimulation with amplitude and latency of response.

I. MATERIAL AND METHODS

An Atlantic bottle-nosed dolphin (*Tursiops truncatus*, adult female, named Kolohe) with no suspected auditory deficiencies, was trained at the Hawaii Institute of Marine Biology facility, Coconut Island, Hawaii to beach itself on a foam mattress, and to accept application of the sound transducer and three skin electrodes. A series of white dots (zinc ointment), spaced 10 cm apart, was applied for each session along a line from the right flipper to the tip of the lower jaw. The reference point was 5 cm below the angle of the mouth. The dots served as landmarks for positioning the sound transducer (see Fig. 1).

The transducer was made from a disc of PZT piezoelectric ceramics (diameter 6.3 mm, thickness 2 mm), backed by corprene. This assembly was placed in a 25-mm-diameter suction cup mold and potted with degassed Uralite 3138 (Hexcel). This compound has a rho-c value (specific acoustic impedance, the product of density and sound velocity) close to that of water (Moffett *et al.*, 1986). On application, the cavity of the cup was filled with water, creating a sound-conducting bridge between the transducing element and the skin. Only the right side of the animal was stimulated.

The ABR electrodes were modified tin/lead alloy plate-shaped electrodes (Dantec 13L71), mounted in 45-mm-diameter suction cups. They were placed, respectively, on the vertex, below the contralateral meatus, and on the melon, using conductive electrode gel to create contact with the skin.

The ABR signal was amplified differentially and bandpass filtered (0.3 to 3 kHz) by a Grass P15 preamplifier before being led through an additional gainblock and a Precision Filters 88A, 130-dB/octave low-pass filter to a Tucker-Davis 16-bit sampling and averaging device. Sampling rate was 25 kHz. An on-line artifact-rejecting algorithm was used to prevent signals with excessive noise from entering the average.

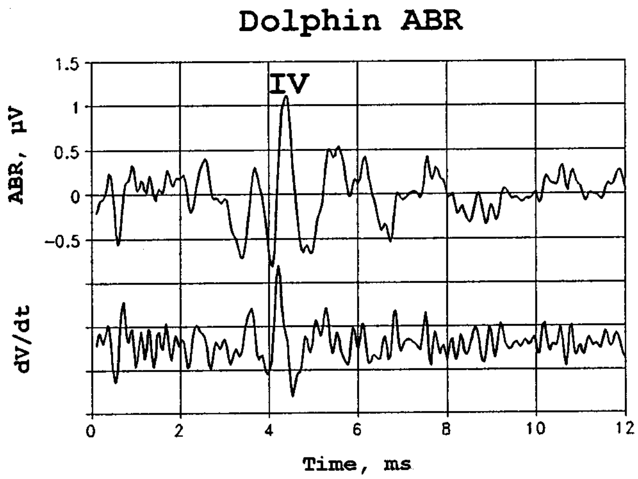

FIG. 2. Example of the ABR signal (top) and its differentiated representation (bottom). Zero on the time axis denotes onset of sound stimulation. Average of 512 stimulations.

The stimulus was a broadband, synthetic, generic porpoise click (Au, 1993), which when filtered by the transmitting response of the transducer had peak energy at 53 kHz and was 3 dB down at 46 and 62 kHz. Repetition rate was 10 clicks per s.

The free-field peak-to-peak level at 1 cm was about 140 dB *re* 1 μPa/V. This signal was generated by a Datel 1200 card, synchronized with the Tucker-Davis unit. Each trial consisted of either 512 or 1024 stimulations, the responses to which were averaged for a period of 12 ms after stimulus onset.

II. RESULTS

A typical recorded ABR waveform is shown in Fig. 2. It is similar to that recorded from submerged dolphins by Ridgeway *et al.* (1981), using far-field stimulation. The ABR signal is a compound, multipeaked signal, generated by auditory neurons in the brainstem, tens of centimeters away from the recording electrodes. The various peaks are believed to reflect the summated activity in the individual neurons of the auditory nerve and brainstem nuclei. The amplitude with our conditions is on the order of microvolts. The most prominent peak (IV in Ridgeway *et al.*, 1981) occurs with a latency of about 4 ms after onset of stimulation.

The input/output functions, when plotted as ABR peak-amplitude versus stimulus intensity, have slopes around 1 μV per 15-dB increase in stimulation. The best dynamic range obtained was 50 dB.

The ABR amplitude depended on point of application. Figure 3 shows a map of interpolated attenuation values required to produce an ABR signal of 1 μV. Best sensitivity was found to sound applied just forward of the pan bone, about 25 cm behind the tip of the lower jaw. Moderate sensitivity was found to sounds applied on the forward portion of the lower jaw and in a posterior region of the pan bone. Stimulation within the mouth, on the internal, lateral side of

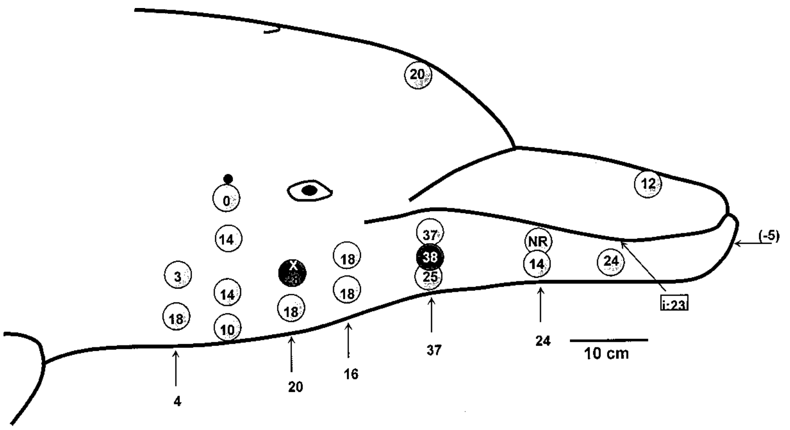

FIG. 3. Points of stimulation (filled circles) with attenuation (dB *re*: fixed reference) required for an ABR-IV yield of 1 μVpp. The point marked ''×'' is the position of minimum delay. The point marked ''38'' (in white) is the point of maximum sensitivity. Numbers below arrows signify attenuation for stimulation on the ventral midline, while the square label shows attenuation for stimulation on the inside of the lower jaw. No ABR could be detected at the point marked ''NR.''

the jaw about 10 cm caudal of the tip and 2 cm below the row of teeth, showed sensitivity equal to that of the outside.

A latency measure was obtained by differentiation of the ABR signal, establishing the point in time of maximal change in neuronal firing. This point is on the rising front of the most prominent peak (IV). The increment used was the clock period (40 μs). The reason for performing this operation is to obtain a measure of latency with a smaller ambiguity than can be obtained from peak determination of the ABR. The sharpening of the response in the time domain of the differentiated waveforms as compared with that of the mother function is illustrated in Fig. 2. Latencies decreased with increased stimulation within a range of 6 to 8.5 μs per dB.

The shortest latency was found for stimulation in the area below the eye. When plotted as relative delay against distance from this point (marked × in Fig. 3), delays are consistently larger than predicted from a linear model of straight-line propagation and the lowest value for velocity of sound propagation in fatty tissues of the dolphin head (Norris and Harvey, 1974).

III. DISCUSSION

The ABR signal is rather variable in waveform, amplitude, and latency. The sources of this variability are many, and their results are cumulative. Simple stochastic ones are to some extent taken care of by the averaging process, but others such as transient noises, differences in transducer coupling, and muscle-tone changes in the animal, contribute in ways that cannot be evaluated, and thus limit the interpretative strength of the data.

Having the experiment done in air helped to ensure that the stimulus was localized to the spot where the suction cup was applied, and not propagated to the animal via some unknown path. Also, point-contact stimulation of an animal outside the medium for which its peripheral auditory system is adapted is questionable. Is it sound or vibration stimulation? What is the effective stimulation level? And what are the consequences of essentially ''loading'' the input impedance of the ear with the very low rho-c value of air instead of the high one of water?

The sensitivity distribution of Fig. 3 is not substantially different from that obtained by Bullock *et al.* (1968) in acute preparations with electrodes implanted directly in the brain stem and stimulation with hand-held transducers, pressed against the surface. Both studies point to the front half of the lower jaw as being the most sensitive area with sound applied via contact transducers. This area appears to be extended somewhat forward relative to the classical acoustic window proposal of Norris, but essentially this study joins those that support the jaw-hearing hypothesis. The best ABR sensitivity was found to sound applied 25 cm behind the tip of the jaw.

The finding of good sensitivity to sound applied to the inner side of the lower jaw is noteworthy for two reasons. One is that it counterindicates a sound-reflective property of the inner side of the jaw. The other reason is that dolphins occasionally are observed to investigate objects by sonar with open mouth. This would indeed seem to require acoustic sensitivity to the inside of the mouth, as confirmed here.

The differences in latency presented in Fig. 4 are likely to be due to differences in sound path, and we thus prefer to use the term delay to describe this effect. The shortest delay is found in an area about 10 cm ventral of the eye, in a region close to, if not identical to, the meatal/bulla region of sound entrance of Popov and Supin (1990). However, this area is at the rear limit of that of best sensitivity. This discrepancy in area location for the two parameters may indicate the presence of a shaded receiving transducer, where input is

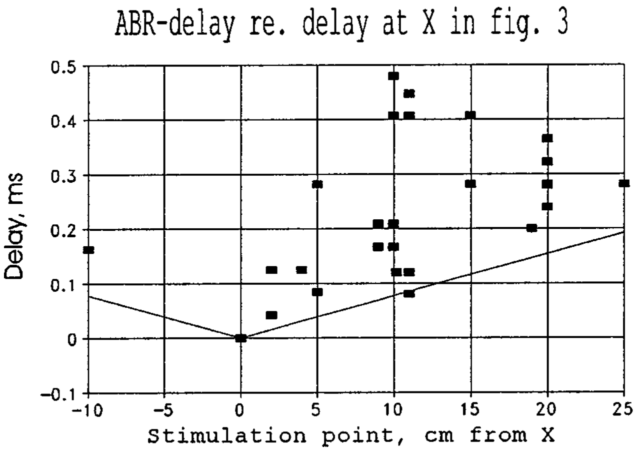

FIG. 4. Delay of the ABR-IV component as a function of distance from point ''×'' in Fig. 3. Stimulation at fixed reference value. The lines are graphical representations of the hypothesis of delay being a linear function of distance from point × in Fig. 3, using a velocity of sound of 130 cm/ms.

weighted according to direction of arrival and position across the aperture of the receiver. In this way, the directional characteristics of the ear can be shaped. Note that delay is increased for stimulation behind point *D*, indicating sound to be routed forward of this point.

Figure 4 demonstrates that delay is consistently larger than expected assuming a constant, low velocity of propagation along a linear path (the jaw). Part of this may be explained by the reference point (at the surface) being displaced from the common point of entry to the auditory pathway. However, unrealistically large values of this displacement (20 cm) are required to fit the data. Also, the assumed propagation velocity of 130 cm/ms, the lowest found in fatty tissues of the dolphin head by Norris and Harvey (1974), may be off, but again only unrealistically low values (<80 cm/ms) can explain the data from this hypothesis. The excessive delays remain at present unexplained.

When evaluating the models, it should be borne in mind that the cross section of the mandible is on the same order of magnitude as the dominant wavelength of *p*-waves (compressional or longitudinal waves, as opposed to transversal and shear waves) in water and soft tissues at 50 kHz (3 cm). A logical consequence of this observation is that models inspired from optical analogies (reflections, refraction, etc.) are problematic, as they require structures that are considerably larger than the wavelength. However, in mixed media with solid components, other sorts of waves than compressional, longitudinal ones can be realized.

IV. CONCLUSION

Good sensitivity to point-applied sound is found in the entire region of the lower jaw, and is best in the middle half of the jaw. The inside of the jaw is as sensitive as is the outside. The question, ‘‘Where is sound entering the auditory system of dolphins?’’ may have to be rephrased into two questions, one dealing with the area of minimum delay and one dealing with the area of minimum attenuation. As these areas seem to differ, a shaded receiver configuration is proposed.

ACKNOWLEDGMENTS

This research was jointly supported by Office of Naval Research (Grant No. N00014-95-1-0605) and the Danish National Research Foundation. This is Hawaii Institute of Marine Biology Contribution No. 1041.

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