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The Role of Asymmetry of the Left and Right External Ear of Bottlenose Dolphin (*Tursiops truncatus*) in the Spatial Localization of Sound

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Abstract—It is generally accepted that Odontoceti lost their external ears (pinnae) in the process of adapting to aquatic habitats. However, their hearing localizes sound with an accuracy of 1° in the frontal and median planes and is directional. These facts indicate the presence of morphological structures functionally performing the role of evolutionarily new external ears adapted to the aquatic environment. The data available to date suggest that this role is played by the left and right row of mental foramina (MFs) and the morphological structures of the rostrum and skull of the dolphin. In this study, for the first time for Odontoceti, the paths of sound travel along MFs and mandibular canals of the lower jaw of bottlenose dolphin (*Tursiops truncatus*) are measured, and the relative time delays of sound between the MF and the degree of their acoustic shielding by the rostrum and skull depending on the localization of sound in space are calculated. It was established that the left and right outer ear form unique temporal and spectral signs of the spatial localization of sound with a maximal accuracy realized rostrally. Localization mechanisms are based on asymmetry, including rostral–caudal and left–right mutually complementary asymmetry of MF architecture, dorsal–ventral asymmetry in the size of the rostrum, as well as rostral–ventral asymmetry in the position of the left and right row of MFs on the rostrum and rostral–caudal asymmetry in the sizes of the rostrum and skull. Thus, unlike the outer ears of terrestrial animals and human beings limited by the auricles, the outer ears of the dolphin are integrated into the streamlined shape of the rostrum and head of the dolphin, which reduces the resistance to its movement from the water side and, most importantly, does not worsen the signal-to-noise ratio of the flow around it in its hearing with increasing speed. Based on the morphology similarity of Odontoceti, it is natural to assume that their MFs and the morphological structures of the rostrum and skull play the role of external ears and form signs of spatial localization of sounds.

Keywords: dolphin (*Tursiops truncatus*), external ears, asymmetry, mental foramina, mandibular canal, rostrum, skull, sound localization, signal/noise

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INTRODUCTION

Localization of sound sources is the ability of human beings and animals to determine the direction to a source of sound in space and the distance to it by ear. The position of the sound source in space is described by the azimuth (the angle between the direction to its source and the direction to the north in the horizontal plane), the elevation angle (the angular height of the source in the vertical plane), and the range.

It is customary for animals to estimate the accuracy of sound localization by the value of the minimum audible angle (MAA) between two sound sources, while they can still determine which of the sources makes the sound. In experiments, when measuring an MAA, a dolphin has usually been trained to determine

the location of the sound source that is presented in a random order to the left or to the right of the separating net. In [1], the dolphin (*Tursiops truncatus*) localized various acoustic signals equally well in both the vertical and horizontal planes with the best localization accuracy and lowest MAAs of $\sim 0.7^\circ$ and 0.9° on signals similar to the dolphin’s echolocation “clicks”, respectively. At tones from 20 to 90 kHz, the MAA was from 2° to 3° , and it was from 2.8° to 4° at tones of 6, 10, and 100 kHz. When the dolphin’s azimuth was shifted relative to the emitters, the MAAs were 1.3° – 1.5° at an azimuth of 15° and $\sim 5^\circ$ at an azimuth of 30° . The results of this study showed for the first time that dolphin hearing may not use interaural intensity differences (IIDs) and interaural time delay differences (ITDs) of sounds for their localization. In the other studies, the localization accuracy was measured

mainly in the horizontal plane, for example, in the bottlenose dolphin (*Tursiops truncatus*), MAA was about 2° at 3, 8, and 10 kHz and $\sim 0.5^\circ$ at 20 kHz [2].

In the echolocation experiment, at the angular discrimination of two arrays (the positive target is a array of four rods and the negative one is a arrays of two rods, with an angular distance between the rods of 2°), the MAA value in the horizontal plane was about 0.25° – 4° and $\sim 1.6^\circ$ at the use of a modified method of constant stimulus [3]. Approximately the same results on MAA measurements were obtained in echolocation experiments with bats [4].

To localize sound in the horizontal plane, terrestrial animals and human beings use binaural and monoaural features [5, 6]. Binaural signs include ITDs and IID of sounds. However, they do not carry information about the elevation angle and range of the sound source and do not explain the listener's capability for monaural source localization [7].

Human auricles play an essential role in localizing sound in the vertical plane, determination of its position as above-below and front-back, and partly for three-dimensional perception [7–9]. Terrestrial echolocating predators, bats (*Chiroptera*), also use signs formed by the auricles when localizing sound in the vertical plane [10]. At the same time, in nocturnal prey birds, owls (*Tyto alba*, *Phodilus bodius*, etc.), spectral signs of localization in the vertical plane at high frequencies are formed by bilateral asymmetry of the outer ears; in some species of owls (*Aegolius funereus*, *Strix nebulosa*, *Strix uralensis*), this asymmetry extends even to the bones of the skull [11, 12].

Odontoceti lost their outer ears (pinnae) during adaptation to aquatic habitats tens of millions of years ago [13]. However, this fact does not yet mean that, over the subsequent tens of millions of years after that, they did not develop new (evolutionarily) external ears adapted with the aquatic habitat. Thus, the directivity of hearing [14] and the high accuracy of sound localization [1–3] indicate the presence in dolphins of morphological structures that functionally play this role.

However, the mechanisms of passive localization of sound sources by cetaceans were not yet elucidated. This is mainly due to the fact that there is no consensus on the pathways and mechanisms of sound conduction to their middle ear [15]. Thus, the following were considered as sound conduction pathways: the external auditory meatus and the middle ear [16], the proximal area of the lateral wall of the mandibular bone [17], the area of “acoustic windows” of the mandible [18], and soft tissues between the left and right half of the mandible [19]. At the same time, it was shown that the left and right row of mental foramens and the morphological structures of the rostrum and skull of the dolphin play the role of the left and right evolutionarily new external ear [20–24].

This paper is aimed at studying the role of the asymmetry of the morphological structures of the left and right external ear of the bottlenose dolphin (*Tursiops truncatus*) in the formation mechanisms of signs of spatial localization of the sound source.

EXPERIMENTAL

Some Prerequisites for Studying the Problem and the Method

To achieve this goal, we used the results of [20–24] obtained in the morphology study of the lower jaw and skull of the dolphin in the light of the known concepts of acoustics and group antennas, as well as the results of experimental studies. In these studies, the bones of the lower jaw and skull (Figs. 1, 4, and 6) of adult bottlenose dolphins (*Tursiops truncatus*) served as the material for research. The morphology of the structures of the lower jaw and skull of the dolphin considered in the study is consistent with the data of [17, 25, 26].

Note that the acoustic properties of MFs and mandibular canals (MCs) of the lower jaw are determined by their size and architecture. The speed of sound in soft tissues (the neurovascular bundle and the fat body, Fig. 1, FB) that fill the canals of the lower jaw is close to the speed of sound in water [27]. Thus, soft tissues serve as a medium for sound propagation through the MF, MC, and FB to the lateral wall of the tympanic–periotic complex. Therefore, further in the text, we will mainly consider the size and architecture of MF and MC.

Here, the results of [20–24] are considered in the light of the nomenclature of the ears of terrestrial animals and human beings.

1. The left and right rows of the MF and the lower and upper jaws, as well as the skull, functionally play the roles of the left and right outer ear of the bottlenose dolphin (*Tursiops truncatus*) completely adapted with the aquat aquatic environment, respectively. The left and right MCs are located between the corresponding external ear and the tympanic membrane of the middle ear (Fig. 1) and play the role of the left and right external auditory canal of the ear of terrestrial animals, respectively. The role of the tympanic membrane and middle ear is played by the corresponding tympanic–periotic complexes [13, 17, 28].

2. The left and right rows of MFs corresponding to the MC and FB (Fig. 1) are the main path along which sound energy from the external environment is transmitted by a traveling wave to the left and right middle ears of the dolphin. The MF and MC in the dolphin-hearing frequency range (0.1–160 kHz) play the role of acoustically “narrow” waveguides and an acoustic catenoidal horn of the evolutionarily new outer ear of the dolphin. Therefore, only a traveling sound wave along the channels can exist in them, which allows us to calculate the path and the corresponding travel time of the front of the sound wave.

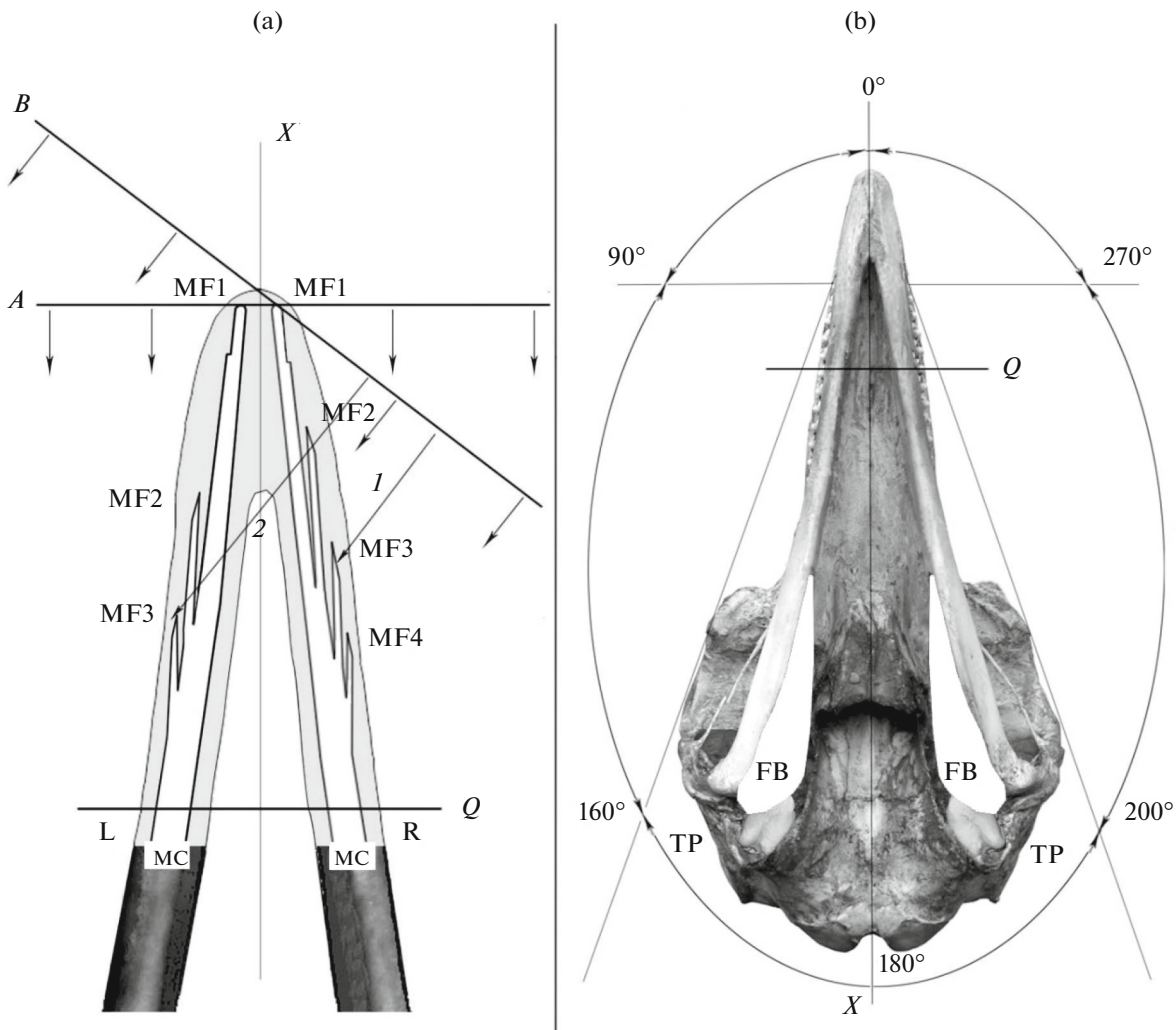


Fig. 1. Rostrum and dolphin skull. (a) Location of the nMF and MC of the left (L) and right (R) external ear (section of the left and right halves of the lower jaw), frontal plane, and dorsal view. The front of a plane sound wave (A) falls rostrally along the longitudinal axis (X) of the mandible and at an angle of 27° to the axis (B). (b) Lower and upper jaw and skull of a dolphin, ventral view. FB, the fat body that fills the MF and MC, is attached to the lateral wall of TP. TP is left and right tympanoperiotic complex (middle and inner ear), respectively. The angles are relative to the middle of the left and right MF rows.

At the same time, in light of the well-known concepts of acoustics and group antennas, the left and right rows of MFs play the role of an array of elementary receivers of a traveling wave antenna (TWA). The sensitivity maximum of a TWA coincides with the direction along which its elementary receivers are located, i.e., the MF. Consequently, the directivity maxima of the dolphin's left and right outer ear coincide with the directivity maximum of corresponding TWA. In the frontal plane, they are directed at an angle of $\sim 0^\circ$ rostrally and in the median plane at an angle of $\sim 7^\circ$ rostral-dorsally, which coincides with the maxima; the directivity characteristic (DC) of the emission of echolocation "clicks" and maximal DC of hearing in the bottlenose dolphin [29, 30].

3. With closed jaws, the transverse dimensions of the left and right outer ear of the dolphin (rostrum and

skull) gradually increase caudally (Figs. 1, 4, and 6) from 3 to 6.5 cm in the frontal plane and from 5 to 7 cm in the median, and further up to 11 and 12 cm, respectively, at the skull; the maximal dimensions of the skull in both planes are ~ 23 cm. In the frequency range of 3–160 kHz, the upper jaw, teeth, and lower jaw of the bottlenose dolphin MF region make up an acoustic screen (AS), the transverse wave dimensions of which increase caudally, $kL > 0.37$ –44–80. The wave dimensions of the skull in this frequency range are $kL > 3$ –144 dorsally-ventrally and laterally, where $k = 2\pi/\lambda$ is the wavenumber, L is the characteristic dimensions of the rostrum and skull, and $\lambda \sim 50$ –0.94 cm is the sound wavelength in this frequency range.

Consequently, the wave dimensions of the dolphin's rostrum fall mainly on the "geometric" back-scattering frequency range, the boundary of which

begins at $kL > 1$, where $k = 2\pi/\lambda$ is the wavenumber, L are the characteristic dimensions of the rostrum, and λ is the sound wavelength. Correspondingly, the rostrum scatters back the incident spectral components of sounds with frequencies above 3–4 kHz, but the sound components below these frequencies bend around the rostrum due to diffraction. In other words, the rostrum shields the sound spectrum at frequencies above 3–4 kHz and plays the role of an equivalent low-pass filter (ELPF) from the side contralateral to the sound. The cutoff frequency of this ELPF and the degree of screening of MF or the degree of spectral sound filtering are determined by the wave dimensions of the rostrum (kL). Therefore, the cutoff frequency of the ELPF decreases, while the degree of filtering increases with increasing sound frequency and the size of this acoustic screen (i.e., for more caudally sounds), respectively.

Similarly, a skull with a slightly larger wave size (kL) begins to backscatter the incident spectral components of sounds with frequencies above 1 kHz, but the components of sounds below these frequencies bend around the skull due to diffraction. Thus, the skull also plays the role of an acoustic screen and ELPF from the side contralateral to the sound.

4. Areas of acoustic light and shadows of the considered morphological structures were determined with allowance for the shape and size of the rostrum (upper and lower jaws) and skull, as well as the wavelength of sounds, in the approximation of “geometric” acoustics.

5. An acoustic length of the rostrum in the region of the left and right MF row (rostrally-caudally) is $L/\lambda \sim 10.7$, where $L \sim 10$ cm and $\lambda \sim 0.94$ cm. The wavelength of the maximal frequencies of the echolocation system and the hearing of the dolphin is ~ 160 kHz; the wave dimension of the rostrum in this area (rostral-caudal) is $kL \sim 62.8$, where $k = 2\pi/\lambda$ is the wavenumber and $L \sim 10$ cm is the characteristic dimensions, with $\lambda \sim 0.94$ cm.

Each linear array of TWA receivers is matched to receive a plane sound wave. In this case, the Fraunhofer zone or “far acoustic field” of the antenna, where the phase difference between the fronts of plane and spherical sound waves is considered to be sufficiently small, starts from distance R to the omnidirectional sound source and is defined as follows:

$$R \geq L^2/\lambda,$$

where $L \sim 10$ cm is the length of the lower jaw of the dolphin in the region of the left and right rows of MF, Fig. 1; $\lambda \sim 0.94$ cm, the wavelength of the maximal frequencies of the echolocation system and the hearing of the dolphin is ~ 160 kHz. Hence, we obtain the estimate: $R \geq 100$ cm.

Therefore, the sound of an omnidirectional source incident on the left and right rows of MFs from dis-

tances greater than about 100 cm is a plane sound wave.

6. It is known that the sound pressure generated by a small source (monopole) of sound (low frequencies, $k^2r^2 < 1$, where $k = 2\pi/\lambda$ is the wavenumber, λ is the wavelength, and r is the radius of the source) does not depend on its shape and is determined only by its volumetric oscillatory velocity V_Ω . In turn, $V_\Omega = SV$, where S is the area of the monopole and V is the oscillatory velocity of the monopole. The weight coefficients that determine the ratio of sound pressure levels in an MF are calculated in accordance with the ratios of the cross-sectional areas of the MF and MC at their junctions. The amplitudes of the sound pressures of the incident, transmitted, and reflected waves at the jump in the cross sections of the waveguide are determined as follows:

$$A_2 = \frac{2\sigma_1}{\sigma_1 + \sigma_2} A_1, \quad B_1 = \frac{\sigma_1 - \sigma_2}{\sigma_1 + \sigma_2} A_1,$$

where A_1 , A_2 , and B_1 are the amplitudes of the incident, transmitted, and reflected waves, respectively, and σ_1 and σ_2 are cross sections of the bordering sections of the MF and MC.

Hence, the calculated normalized values of the weight coefficients determining the ratio of sound pressure levels (SPLs) are 1.0, 0.37, and 0.21 in MF1–MF3 of the left outer ear and 0.95, 0.29, 0.19, and 0.06 in MF1–MF4 of the right outer ear, respectively.

The duration of the actual sound in MFs is the same, and we take it equal to unity in the calculations.

Taking into account the results discussed above and obtained in [20–24], it is not difficult to see that the sequence and degree of illumination of each MF with sound or shielding by the rostrum and skull are determined by the shape and acoustic dimensions of the rostrum, the architecture of the MF, the rostral-caudal asymmetry of the acoustic dimensions of the rostrum and skull (Figs. 1, 6), most importantly, the location of the sound source relative to the rostrum and skull in space. At the same time, each MF transmits some of the energy of this sound or a partial sound with a certain level of sound pressure (in accordance with the weighting factor, see above) to the corresponding MC. Partial sounds propagate along the left and right MC to the left and right middle ear (the tympanoperiotic complex) with different relative time delays and different degrees of spectral filtration, respectively. These prerequisites make it possible to suppose that the morphological structures of the dolphin’s peripheral hearing—its left and right outer ears—form the spectral and temporal signs of the spatial localization of the sound source relative to the dolphin.

To study the formation mechanisms of signs of spatial localization of a sound source by the outer ears of a dolphin, we measured and analyzed here the change in the travel time of the front of a plane sound wave through each MF and the degree of their screening

Table 1. The results of measuring the paths of the front of a plane sound wave through each MF up to section *Q* (Fig. 1) and its spectral filtering depending on the spatial localization of sound

Localization of sound relative to the external ears of a dolphin,	The measured paths of the sound wave front through each MF up to section <i>Q</i> , Fig. 1, mm. The first term, the path from the front of the sound wave to nMF. The second term is the path inside nMF+MC up to section <i>Q</i> . The sequence of MFs (from left to right) is shown as the front of a plane sound wave runs through them						
Rostrally, FP (Fig. 1a, <i>A</i>)	rMF1 0 + 126.3	lMF1 0 + 126.3	rMF2 34.8 + 91.5	lMF2 51.3 + 75	rMF3 66.3 + 60	lMF3 80.7 + 45.6	rMF4 85.8 + 40.6
Caudally 180°, FP (Fig. 1)	rMF4 0 + 40.6 SF	lMF3 5.2 + 45.6 SF	rMF3 20.9 + 60 SF	lMF2 35 + 75 SF	rMF2 45.9 + 91.5 SF	lMF1 85.5 + 126.3 SF	rMF1 85.5 + 126.3 SF
27°, FP (Fig. 1a, <i>B</i>)	rMF1 0 + 126.3	rMF2 22.2 + 91.5	rMF3 42.6 + 60	rMF4 56.2 + 40.6	lMF1 5.4 + 126.3	lMF2 d87.6 v60.8 r59.5 + 75 SF	lMF3 d190 v96.5 r91.2 + 45.6 SF
Ventrally 270°, MP (Fig. 6)	rMF4 0 + 40.6	lMF3 0 + 45.6	rMF3 0 + 60	lMF2 0 + 75	rMF2 0 + 91.5	lMF1 6.6 + 126.3	rMF1 5.8 + 126.3
Dorsally, 90°, MP (Fig. 6)	rMF1 0 + 26.3 SF	lMF1 2.1 + 126.3 SF	rMF2 8.7 + 91.5 SF	lMF2 8.7 + 75 SF	rMF3 8.7 + 60 SF	lMF3 8.7 + 45.6 SF	rMF4 8.7 + 40.6 SF
Right, 270°, TP (Fig. 4)	rMF4 0 + 40.6	rMF3 3.1 + 60	rMF2 10.2 + 91.5	rMF1 18.9 + 126.3	lMF1 26.5 + 126.3	lMF2 d82.2 v48.1 + 75 SF	lMF3 d92.2 v56.9 + 45.6 SF
Left, 90°, TP (Fig. 4)	lMF3 0 + 45.6	lMF2 4.8 + 75	lMF1 17.3 + 126.3	rMF1 24.9 + 126.3	rMF2 d83 v43.7 + 91.5 SF	rMF3 d88 v51.8 + 60 SF	rMF4 d94 v55.9 + 40.6 SF

SF is the spectral filtering, MC is the mandibular canal, rMF is the right mental foramen, lMF is the left mental foramen, FP is the frontal plane, MP is the median plane, TP is the transverse plane; and d, v, and r are the path of sound (diffraction) to contralateral MFs from the dorsal, ventral, and rostral sides of the rostrum, respectively.

from the moment the sound front hits the MF closest to it, depending on the sound localization in space. To do this, the sound paths from the front of a plane sound wave through each MF to corresponding section *Q* were measured (Fig. 1, Table 1), while the degree of shielding of the MF by the rostrum and skull was determined depending on the location of the sound in space.

The necessary measurements were made in Photoshop CS3 using the ruler tool. In this case, the measurement accuracy is hundredths of a centimeter. Taking it into account that the minimum wavelength of the highest frequency of dolphin sounds (~160 kHz) is about 0.94 cm and the minimal calculated ITDs of dolphin hearing to obtain an MAA of 1° is ~1.3 μs [31], the accuracy of path measurements of the range of sound in the present study is sufficient. The travel time of sound through each MF was calculated with allowance for the corresponding measured path and the speed of sound in the water and soft tissues of the dolphin that is equal to 1500 m/s [27].

The calculated travel time of sound along the first MFs of the left and right outer ear to corresponding sections *Q* (Fig. 1) is 84.2 μs and to the lateral walls of the left and right tympanoperiotic complex is ~273 μs.

RESULTS AND DISCUSSION

The results of measuring the paths of partial sounds to section *Q* (Fig. 1) and the degree of shielding of the MF depending on the spatial localization of the sound source relative to the left and right outer ear of the bottlenose dolphin (*Tursiops truncatus*) are given in Table 1. For convenience of interpreting the obtained results, the values of the travel paths (Table 1) were recalculated into travel times and presented as a dependence of the relative time delays of partial sounds on the spatial localization of sound in the frontal, transverse, and median planes (Figs. 2, 3, 5, and 7).

Let consider the formation mechanisms of signs of sound localization by the left and right outer ear of a dolphin in each plane.

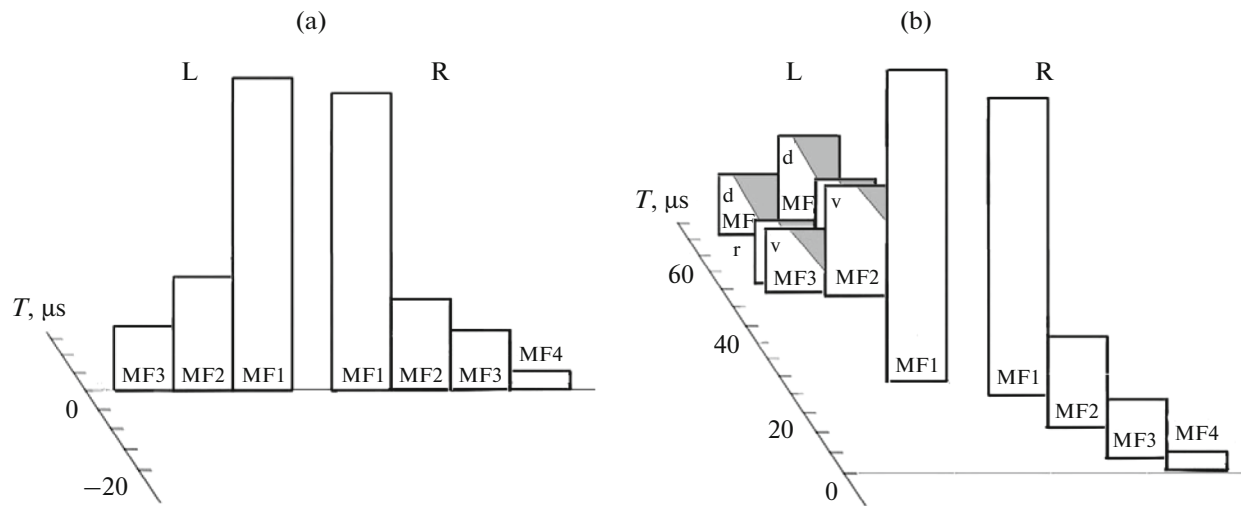


Fig. 2. Relative delay time of partial sounds of MF1–MF3 of the left (L) and MF1–MF4 of the right (R) outer ear (a) for the rostral and (b) at an angle of 27° to the X axis of the sound in the frontal plane (Fig. 1a), respectively. The height of the rectangles is proportional to the relative sound pressure levels of partial sounds, and the width of the rectangles is equivalent to the dolphin’s hearing frequency band (1–160 kHz). The results of spectral filtering of partial sounds are shaded. The duration of the sound in MF is the same and is not conditionally shown. T is the delay time in microseconds. d , r , and v are the sound diffraction from the dorsal, ventral, and rostral sides of the outer ears (rostrum) to contralateral MFs, respectively.

Frontal Plane

A plane sound wave from a rostral sound source is incident on the left and right outer ears of a dolphin in the frontal plane along the longitudinal X axis (Fig. 1a, A) while the sound wave front runs the same distance through each MF to section Q of the left and right MC

and to the left and right middle ear, respectively. In this case, all MFs are illuminated by sound, and the relative delay time of partial sounds is about $0 \mu\text{s}$, i.e., all partial sounds running through MFs are added in section Q of the left and right MC and, consequently, in phase on the left and right middle ears of the dolphin (Figs. 2a, 3). It should be noted that the first MFs of the left and right outer ear will be equally illuminated by sound when it is localized in a wide sector of the rostral–lateral angles (110° – 0° – 250° , Fig. 1b), and, they will be shielded by the rostrum and, then, by the skull only when the sound is shifted to the area of the lateral–caudal angles. Unlike this, even at a minimal ($\sim 1^\circ$ – 2°) movement of the sound source to the left or to the right of 0° , the degree of illumination of remaining MFs of the left and right outer ear changes to the opposite (increases on the left and decreases on the right, with increasing angle, or vice versa, respectively, Fig. 1), due to changes in the degree of MF shielding by the rostrum and degree of spectral filtering of partial ELPF sounds. We can assume that the considered mechanism of changing the acoustic illumination and screening of an MF provides the maximal localization accuracy in the direction of $\sim 0^\circ$. In this case, partial sounds run to left and right sections Q (Fig. 1) and to the left and right middle ears already with differences in spectrum levels at frequencies above 3–4 kHz and a minimal difference in the relative time delays of partial sounds. Thus, the maximal accuracy of sound-source localization in the frontal plane is realized in the direction of $\sim 0^\circ$ (Fig. 1). The obtained result agrees with the direction of the maximal DC of hearing and the emission of dolphin echolocation “clicks” [29, 30].

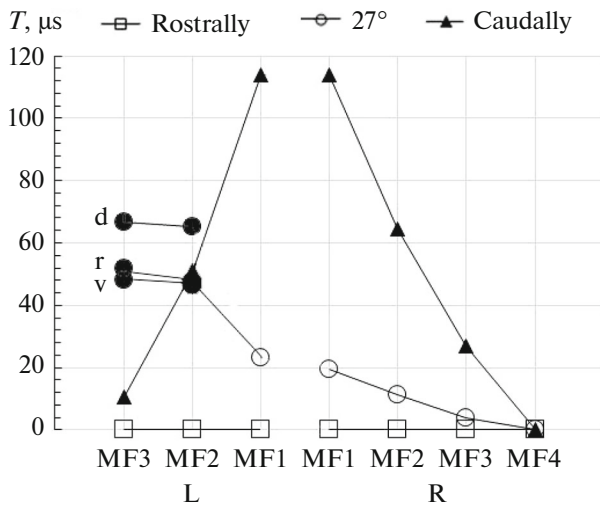


Fig. 3. Relative delay time of partial sounds of MF1–MF3 of the left (L) and MF1–MF4 of the right (R) outer ear, for the rostral and caudal, and at an angle of 27° to the X axis of the sound in the frontal plane (Fig. 1), respectively. The ordinate axis is delay time T in microseconds. The abscissa axis is the numbers of corresponding MFs. Markers that are not filled (filled) with black mean sound illumination (screening with a rostrum) of corresponding MFs. Notations d , r , and v are indicated in Fig. 2.

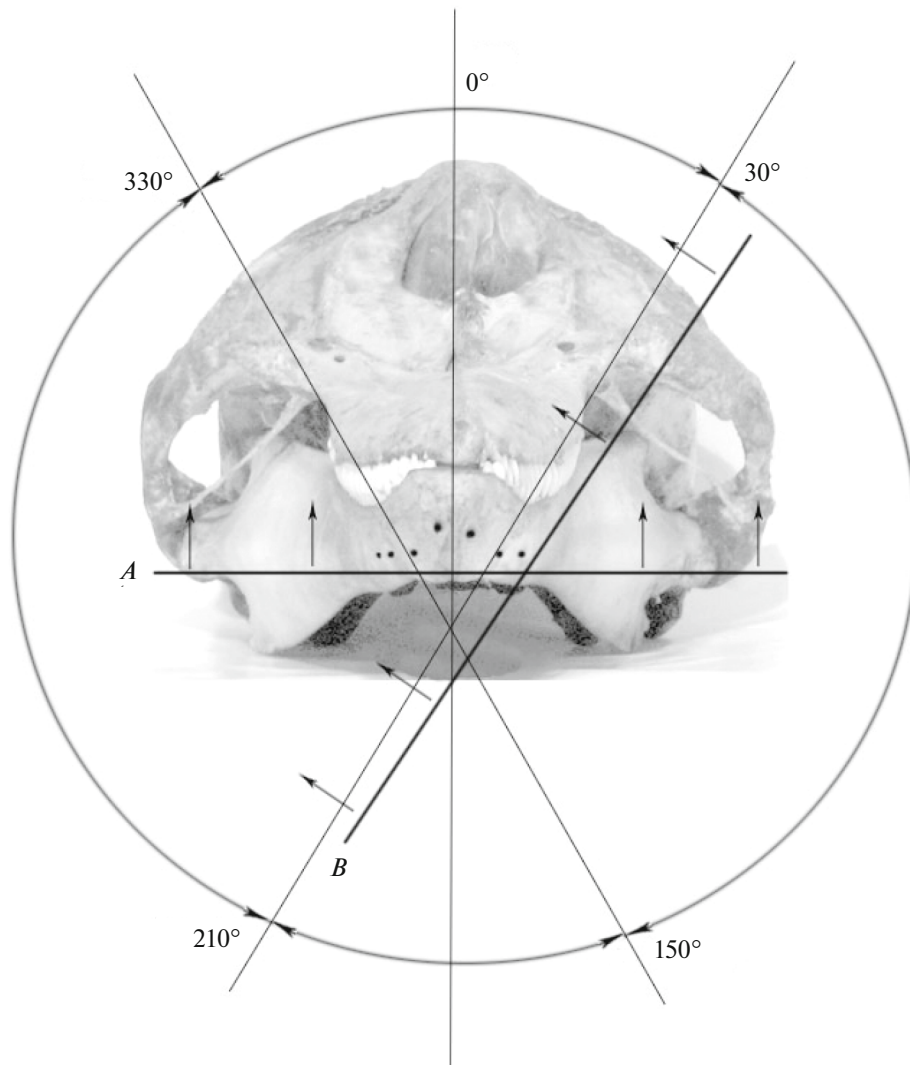


Fig. 4. Rostrum and skull of a dolphin (left and right external ear), rostral view, transverse plane. (*A*) the front of a plane sound wave falls on the outer ears ventrally, and (*B*) ventrally–laterally. The angles are relative to the middle of the left and right MF rows.

When the sound source moves relative to the rostrum to the left (in the range of angles up to 200°) or to the right (up to 160°) in the frontal plane (Fig. 1b), with increasing angle, these differences in the relative delay time and the degree of illumination and shielding of the MFs of the left and right outer ear by sound increase. As an example, signs of localization that are formed by the external ears of a dolphin when the sound source is positioned at an angle of 27° relative to the X axis in the frontal plane are shown (Fig. 1a, *B*, and Fig. 2b). In this case, the sound travels a shorter path through caudal MFs of the right half of the lower jaw to section Q than through rostral MFs (Table 1). Therefore, partial sounds run to section Q through rostral MFs (and to the corresponding middle ear) with a time delay increasing up to $20 \mu\text{s}$ (IMF1 and rMF1) relative to MF4 (Figs. 2, 3). In other words, the relative delay time of partial sounds changes due to the

change in the paths from the front of the plane sound wave to each MF depending on the localization of the sound. Moreover, MFs of the right outer ear are ipsilateral to the sound source and are illuminated by sound (Figs. 1a, *I*) while MF2 and MF3 of the left outer ear are located contralateral to the source and the degree of their shielding by the rostrum increases with increasing angle. Only low-frequency (below 3–4 kHz) sound components that flow around the rostrum from the dorsal (d), ventral (v), and rostral (r) sides as a result of diffraction (Fig. 1a, 2, and Fig. 2b) will fall on these MFs and run through them up to section Q . In this case, the sound path to contralateral MFs and the relative delay time of partial sounds increase to 40–60 μs . The high-frequency (above 3–4 kHz) components of sounds are screened by the rostrum, which plays the role of an ELPF. The cutoff frequency of this filter is $\sim 3\text{--}4$ kHz. In Fig. 2b, the cutoff frequency of

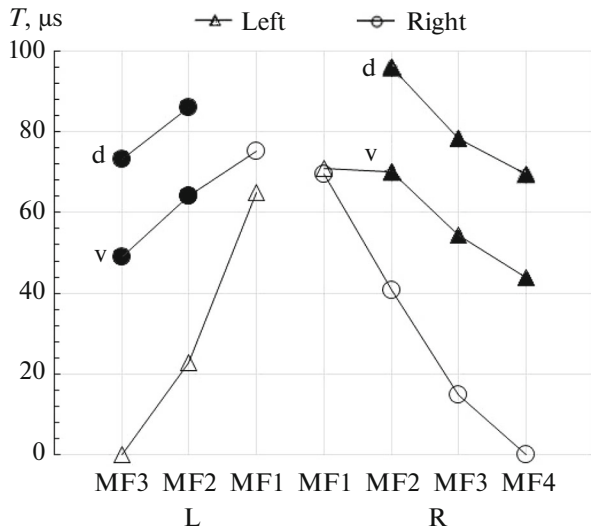


Fig. 5. Relative delay time of partial sounds MF1–MF3 of the left (L) and MF1–MF4 of the right (R) outer ear, for lateral sound (left or right), in the transverse plane (Fig. 4), respectively. The ordinate axis is delay time T in μ s. The abscissa axis is the numbers of corresponding MFs. Markers that are not filled (filled) with black mean sound illumination (screening with a rostrum) of corresponding MFs. Notations d, r, and v are indicated in Fig. 2.

the ELPF and the degree of spectral filtering are conditionally shown as the shaded part of the rectangles of partial sounds.

When the sound source is shifted in the frontal plane to the lateral position on the right (90° , Fig. 1), the delay time of partial sounds (rMF1) relative to MF4 continues to increase up to 70 and 88 μ s for the sound components that flow around the rostrum with the dorsal (d) and ventral (v) side (IMF2 and IMF3), respectively (Fig. 5), along with an increase in the degree of shielding of contralateral caudal MFs. At further displacement of sound relative to the rostrum in the frontal plane, the relative delay time of partial sounds and the degree of spectral filtration of the MF increase and reach a maximum at the caudal position of the sound source ($\sim 114 \mu$ s, Fig. 3).

When the sound source is localized in the angle region of 160° – 180° – 200° (Fig. 1b), the skull is located in the path of the sound. Therefore, only the low-frequency components of the sound, which flow around the skull due to diffraction, fall on the MFs. Its high-frequency components are shielded by the skull, which plays the role of an ELPF with a cutoff frequency of ~ 1 kHz.

When the sound source is shifted in the frontal plane from 200° to 360° (Fig. 1b), the relative delay

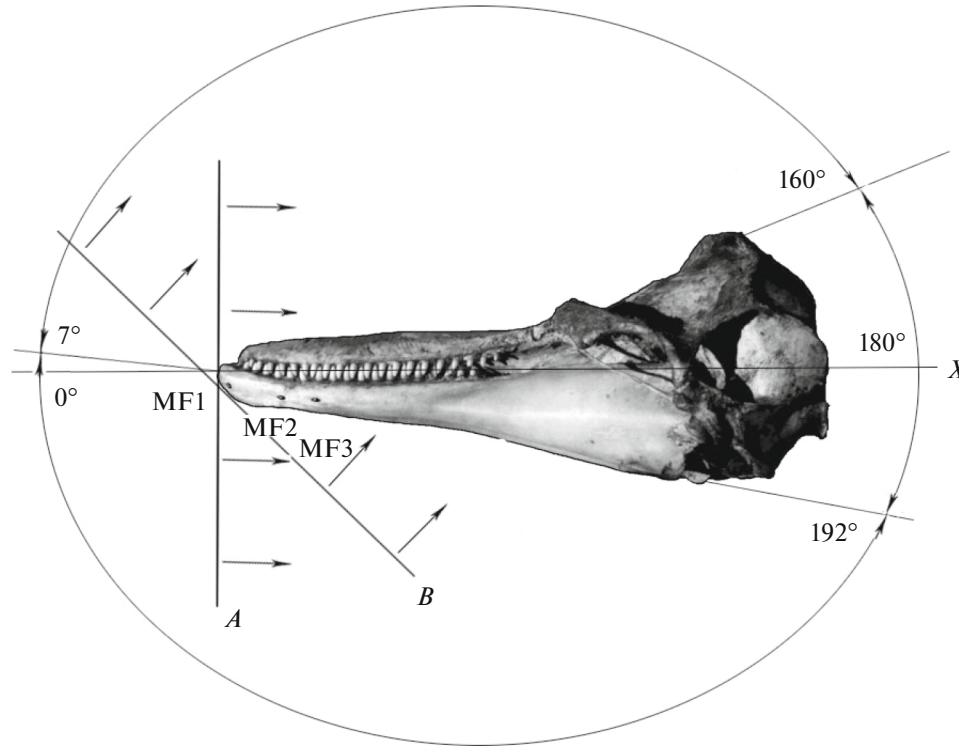


Fig. 6. Rostrum and skull of a dolphin (left outer ear), lateral view, left side, median plane. (A) The front of a plane sound wave is incident on the external ears rostrally–dorsally, at an angle of 7° , and (B) ventrally–rostrally. The angles are indicated relative to the X axis in the middle of the left MF row.

time of partial sounds decreases and the degree of screening of caudal MFs of the right outer ear changes. For example, at the lateral position of the sound source on the left (270° , Fig. 1b), the delay time of partial sounds (IMF1) relative to IMF3 decreases to 67 and to $95 \mu\text{s}$ for the contralateral sound components (rMF2–rMF4) that flow around the rostrum with the dorsal (d) and ventral (v) sides, respectively (Fig. 5). In this case, the sound incident on rMF2–rMF4 is screened by the rostrum. At further movement of the sound source up to the rostral direction, the relative delay time of partial sounds decreases and the degree of shielding of the MF decreases when they are all illuminated by sound and the differences in the relative delay time of partial sounds are minimal (Figs. 1–3).

Thus, for any location of the sound source in the frontal plane relative to the dolphin, its left and right outer ears form unique temporal and spectral signs of the localization of this sound.

The obtained results indicate that the maximal difference between the signs of localization of the rostral and caudal sound (Fig. 3), as well as the left and right sound (Fig. 5), is determined by the rostral–caudal and left–right mutually complementary asymmetry of the MF architecture (Fig. 1a) in the frontal plane, rostral–caudal asymmetry of the sizes of the rostrum and skull (Figs. 1 and 6), as well as large wave sizes ($kL \sim 62.8$) and large acoustic length ($L/\lambda \sim 10.7$) of the left and right outer ear (rostrum) in the MF region.

Transverse Plane

Based on the shape of the rostrum of the dolphin and the MF architecture, it can be concluded that the first MFs of the left and right outer ear are almost equally illuminated by sound in a wide sector of the lateral–ventral angles of the transverse plane (30° – 180° – 330° , Fig. 4), and they are shielded by the rostrum only when the sound is shifted to the dorsal angles (330° – 0° – 30° , Fig. 4). Unlike this, other MFs of the left and right outer ear are simultaneously illuminated by sound only in the region of the ventral positions of the sound source in the transverse plane (150° – 180° – 210° , Fig. 4). At the same time, at a ventral sound source (180° , Fig. 4), the relative delay time of the partial sounds IMF1 and rMF1 reaches 62 and $64 \mu\text{s}$, respectively (Fig. 7). The spectral filtering of all MFs is insignificant (based on the wavelength of sounds and the incidence angle of sound on the walls of the lower jaw). In this case, the relative delay time of partial sounds in this region varies depending on the localization of the sound source due to a change in the paths of their travel from the front of a plane sound wave to each MF (Figs. 4, A and B).

If the sound source is located at an angle of 210° (Fig. 4) relative to the rostrum of the dolphin in the transverse plane, the MF of the right outer ear is illuminated by sound and MF2 and MF3 of the left outer

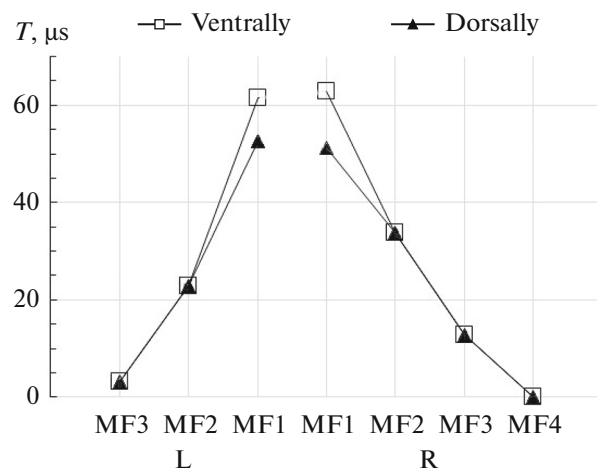


Fig. 7. Relative delay time of partial sounds MF1–MF3 of the left (L) and MF1–MF4 of the right (R) outer ear for ventral and dorsal sounds in the median plane (Fig. 6), respectively. The ordinate axis is the delay time T in microseconds. The abscissa axis is the numbers of corresponding MFs. Markers that are not filled (filled) with black mean sound illumination (shielding by a rostrum) of corresponding MFs.

ear will be on the border of the acoustic light of the source and the shadow of the rostrum. When the sound source moves in the transverse plane to the lateral position on the right (270° , Fig. 4), all MFs of the right outer ear are illuminated by sound while the degree of screening and spectral filtering of the sound incident on contralateral MFs of the left outer ear increases. In this case, the relative delay time of partial sounds increases (Fig. 5) up to $70 \mu\text{s}$ (rMF1) and up to $87 \mu\text{s}$ for the contralateral sound components (IMF2–IMF3) enveloping the external ears from the dorsal (d) and ventral (v) sides, respectively. At further displacement of sound in the transverse plane up to 330° (Fig. 4), the degree of screening by the rostrum of the MF of the left outer ear and the degree of their spectral filtration will increase. The relative delay time of partial sounds also increases depending on the localization of the sound source due to a change in the path from the front of the plane sound wave to the MF. When the sound source moves to the angle region of 330° – 0° – 30° , all MFs gradually fall into the region of acoustic shadow created by the dorsal–ventral asymmetry of the rostrum shape and the asymmetric rostral–ventral location of MFs of the left and right rows of MFs on the rostrum (Figs. 1, 4, and 6). At a dorsal sound source (0° , Fig. 4), all MFs are shielded by the rostrum, and the sound is incident on MF due to diffraction. In this case, the high-frequency components of sounds (above 3–4 kHz) are screened by the rostrum, which plays the role of an acoustic screen and ELPF and reduces the level of high-frequency sound components (Fig. 7).

When the sound source moves in the transverse plane relative to the rostrum to the lateral position on the left (90° , Fig. 4), all MFs of the left outer ear are illuminated by sound, but the degree of screening and spectral filtering of the sound incident on contralateral MFs of the right outer ear increases (Fig. 5). In this case, the relative delay time of partial sounds increases to $64 \mu\text{s}$ (rMF1) and up to $95 \mu\text{s}$ for the contralateral sound components (rMF2–rMF4) flowing around the rostrum from the dorsal (d) and ventral (v) sides, respectively.

When the sound source moves in the transverse plane relative to the outer ears to the ventral position (180° , Fig. 4), the sound illumination of the MF of the left outer ear remains. In this case, the degree of shielding of the MF of the right outer ear will decrease because the ventral sound diffraction paths to contralateral MFs around the rostrum are reduced, and the degree of illumination of left and right MFs is equalized (Fig. 7). The relative delay time of partial sounds also varies with the angle (Figs. 5, 7) due to a change in their paths from the front of a plane sound wave to MF (Figs. 4, A and B) depending on the MF architecture.

Thus, for any location of the sound source in the transverse plane relative to the dolphin, its left and right outer ears form unique temporal and spectral signs of the localization of this sound.

The obtained results indicate that the maximal difference between the signs of localization of the dorsal and ventral sound (Fig. 7) is determined by the dorsal–ventral asymmetry of the rostrum size in the MF region (the dorsal part of the rostrum is wider than the distance between the left and right rows of MF) and the rostral–ventral asymmetry of the location of the left and the right row of MF on the rostrum (Figs. 4, 6), as well as large wave sizes ($kL \sim 62.8$) and large acoustic length ($L/\lambda \sim 10.7$) of the rostrum in the MF region. However, the maximal difference in signs of localization of the left and right sound (Fig. 5) is determined by the left–right mutually complementary asymmetry of the MF architecture (Fig. 1) in the frontal plane, as well as by the large wave sizes and large acoustic length of the rostrum in the MF region.

Median Plane

If a plane sound wave of a sound source in the median plane falls on the outer ears of a dolphin from the direction of the maximal DC of hearing and the emission of the dolphin's echolocation "clicks" of 7° [29, 30] (Fig. 6, A), all MFs are located ipsilateral to the sound source, illuminated by sound, and MF screening and, consequently, spectral filtering of partial sounds do not occur. Signs of localization in this case are formed in the same way as for rostral sound in the frontal plane (Fig. 1a, A; Figs. 2a, 3). It should be noted that the first MFs of the left and right outer ear are almost equally illuminated by sound when it moves

in a wide sector of dorsal-rostral–ventral angles, 90° – 0° – 220° (Fig. 6), and only when the sound is shifted to the area dorsally-caudal-ventral angles, they are shielded by the rostrum and skull. Unlike this, at a minimal (~ 1 – 2°) movement of the sound source more dorsal or ventral of 7° (Fig. 6), the degree of illumination of the remaining MFs of the left and right outer ear changes in the same direction (decreases or increases, respectively) due to a change in the degree of screening of these MFs by the rostral part of the lower jaw that is hung over the MF (Fig. 6), which has large wave sizes, a large acoustic length, and asymmetric curvature (dorsally wider). It can be supposed that the considered mechanism of changing the acoustic illumination and screening of the MF provides a maximal localization accuracy in the direction of $\sim 7^\circ$. In this case, partial sounds run up to sections Q (Fig. 1) and to the corresponding middle ear already with differences in the degree of spectral filtering and minimal differences in relative time delays. Thus, the maximal accuracy of sound source localization in the dolphin in the median plane is realized in the direction of $\sim 7^\circ$ (Fig. 6).

At further displacement of the sound source in the median plane (dorsal) relative to the rostrum (the X axis (Fig. 6)), the degree of screening of caudal MFs by the asymmetric rostral part of the lower jaw (on both sides) increases. It should be noted that rMF1 and lMF1 begin to be shielded by the asymmetric dorsal edge of the mandible only in the dorsal (90° , Fig. 6) position of the sound source when all other MFs are shielded due to the dorsal–ventral asymmetry of the rostrum. In this case, the relative time delays of the partial energies of sound (lMF1 and rMF1) reach 53 and $51 \mu\text{s}$, respectively (Fig. 7), all MFs are screened by the rostrum, and sound is incident on them as a result of diffraction. When the sound source is shifted relative to the rostrum to the region of caudal angles (160° – 180° – 192° , Fig. 6), the degree of shielding of all MFs and the relative time delays of partial sounds increase due to the dorsal–ventral asymmetry of the rostrum and the rostral–ventral asymmetry of the location of the left and the right row of MF on the rostrum, as well as rostral–caudal asymmetry of the MF architecture, rostrum, and the dolphin skull, and reach maximal values at a caudal sound source, as in the frontal plane (Fig. 3). When shielding the MF, spectral filtering of partial sounds that is determined by the degree of their shielding occurs.

When the sound source moves relative to the rostrum to the ventral position (from 192° to 270° , Fig. 6), the degree of MF shielding and the relative time delays between partial sounds decrease (Figs. 6, 7) and, when it reaches the direction of maximal localization accuracy (7° , Fig. 6), the relative time delays of partial sounds and the degree of MF screening are minimal (Figs. 1–3).

Thus, for any location of the sound source in the median plane relative to the dolphin, its left and right outer ears form unique temporal and spectral signs of the localization of this sound.

The obtained results indicate that the maximal difference in the signs of localization of rostral and caudal sound in the median plane does not differ from those in the frontal plane (Fig. 3) and is determined by the rostral–caudal complementary asymmetry of the MF architecture in the frontal plane (Fig. 1), large wave sizes ($kL \sim 62.8$), and large acoustic length ($L/\lambda \sim 10.7$) of the rostrum in the MF region, as well as rostral–caudal asymmetry of the rostrum and skull of the dolphin (Figs. 1, 6). However, the maximal difference between the signs of localization of the dorsal and ventral sound (Fig. 7) is determined by the dorsal–ventral asymmetry in the size of the rostrum in the MF region (the dorsal part of the rostrum is wider than the distance between the left and right MF rows) and the rostral–ventral asymmetry in the location of the left and right MF rows on the rostrum (Figs. 4, 6), as well as large wave sizes and large acoustic length of the rostrum in the MF region.

Formation Mechanisms of Signs of Spatial Localization of Sound by External Ears in a Dolphin

The results obtained here indicate that the main factors determining the mechanisms of the formation of unique temporal and spectral features of the spatial localization of sound in the dolphin's hearing (Figs. 2, 3, 5, and 7) are the asymmetry of the morphological structures of its external ears (Figs. 1, 4, and 6). Interestingly, that among terrestrial animals, the bilateral asymmetry of the external ears of nocturnal prey birds is the main factor determining the mechanisms for the formation of signs of sound localization in the vertical plane only [11, 12].

In the formation of temporal signs of sound localization by the external ears of a dolphin, the main role is played by the rostral–caudal and left–right asymmetry of the MF architecture, large wave sizes, and large acoustic length of the rostrum and skull (Figs. 1, 4, and 6). At the same time, in the formation of spectral signs of sound localization by the outer ears of a dolphin, the main role is played by: rostral–caudal and dorsal–ventral asymmetry in the size of the rostrum and skull and the asymmetric rostral–ventral position of the left and right MF rows on the rostrum (Figs. 1, 4, and 6).

Thus, unlike the external ears of terrestrial animals and human beings limited by the auricles, the considered mechanisms of formation of temporal and spectral signs of sound localization indicate that the external ears of the dolphin are integrated into the streamlined shape of the rostrum and head. Due to the fact that Odontoceti acquired streamlined body shapes as a result of adaptation to the aquatic habitat [28], the

measured flow mode along the upper and lower jaws in the rostrum region, as well as along the dolphin's melon, remains laminar in the velocity range of 1–5 m/s (or 3.6–18 km/h) [34, 35]. Consequently, the streamlined shape of the dolphin's outer ears reduces the resistance to its movement from the water side and, very importantly, does not worsen the signal-to-(noise of the flow) ratio in the hearing with an increase in its movement speed, at least up to 18 km/h. At the same time, the laminar mode of the flow around the melon will not distort the sounds emitted through it in the same range of swimming speeds of the dolphin.

The results of this study indicate that the mechanisms for the formation of unique signs of the spatial localization of the sound source are realized in the dolphin at the level of the external ears. When a plane sound wave front falls on them, three MFs of the left outer ear and four MFs of the right outer ear form sequences of three and four partial sounds with unique high-frequency levels and unique relative time delays depending on the spatial localization of this sound (Figs. 2, 3, 5, and 7), which are transmitted via the left and right MCs to the left and right middle ear, respectively. Thus, the dolphin's hearing only needs to decode these sequences of partial sounds in order to localize the source of the sound in space and interpret the sound.

Unlike this, the external ears of a person, the auricles, form signs of sound localization, mainly in the vertical plane, and determine its position above–below and front–back [7–9] while signs of sound localization in the horizontal plane are formed as a result of processing its IID and ITD at higher levels of the auditory system. These facts indicate a fundamental difference in the formation mechanisms of signs of spatial localization of sound, as well as a difference in the mechanisms of binaural hearing in dolphins and human beings, which also follows from the results of [1] and requires a further study.

The maximal accuracy of the mechanisms of sound localization considered here is realized in the frontal plane of the dolphin rostrally at an angle of $\sim 0^\circ$ (Fig. 1), and in its median plane rostrally–dorsally at an angle of $\sim 7^\circ$ (Fig. 6), which is consistent with the direction of the maximum of the DC of the emission of echolocation “clicks” and the maximum of the DC of hearing in the bottlenose dolphin [29, 30], as well as with the results of experimental measurements of the accuracy of sound localization in a dolphin [1] and the direction of the DC maximum of its left and right TWAs [21]. The left and right MF rows, maximal wave size, and acoustic length of the outer ears, as well as the maximal dimensions of the rostrum and skull of the dolphin, are oriented in the same direction (Figs. 1, 6). Moreover, the sound incident on the external ears from the direction of maximal localization accuracy arrives in phase at the left and right middle ears of the dolphin without relative time delays of

its partial sounds (Figs. 2, 3) while there is no screening of MF and spectral filtering of the partial sounds transmitted by them. This feature of the localization mechanism is of paramount importance for the function of the dolphin's echolocation system since from this direction in space, the maximal levels of reflections (echoes) of probing signals ("clicks") of the dolphin's echolocation system from food items, relatives, and various underwater objects return, which is fundamentally important for a fine analysis of their echoes. It can be assumed that, in this case, all partial sounds are added in phase in the dolphin's hearing, which maximizes the accuracy of echo (sound) perception and the sensitivity of hearing. In this case, based on the ratio of the maximal relative levels of sound pressures of partial sounds (Fig. 2), the gain in in-phase addition of partial sounds can reach around two times.

Many researchers have noted that, when solving echolocation and auditory problems, dolphins scanned with their rostrum (left to right and up to down) [30, 33]. In the light of the results obtained here, it can be supposed that they were more accurately positioning the maximal accuracy of hearing localization in the direction of the echo (sound) in this way.

The spectral and temporal mechanisms of spatial localization of sound in the bottlenose dolphin (*Tursiops truncatus*) considered in this study are consistent with the spectral and temporal characteristics of its acoustic signals [30] and the results of experimental measurements of MAA [1–3]. For example, acoustic signals such as echolocation "clicks" (or their echo) are localized by the dolphin with a maximal accuracy; in this case, the MAAs are less than 1° in the frontal and median planes [1, 3]. This can be explained by the fact that echolocation "clicks" (and their echoes) have spectral components in almost the entire dolphin hearing frequency band [30, 32]. The duration and rise time of the front of "clicks" (and their echo) are the smallest among dolphin's acoustic signals. Consequently, the outer ears of the dolphin form all the potential spectral and temporal signs of the localization of these signals shown in this study. For signals that are less broadband and have a longer rise time, the accuracy of their localization deteriorates to varying degrees, which can be seen by comparing the spectral–temporal characteristics and the localization accuracy of various signals in experiments [1, 2].

At the same time, the accuracy of active localization of echo sources in echolocation experiments [3] and the accuracy of passive localization of sound sources in auditory experiments [1, 2] are consistent. This indicates that, in both cases, the dolphin uses the mechanisms of passive spatial localization of sound considered in this study.

It is interesting that relative SPLs of partial sounds of the actual sound are constant and determined by weighting factors: 1, 0.37, and 0.21 for MF1–MF3 of the left outer ear and 0.95, 0.29, 0.19, and 0.06 for

MF1–MF4 of the right outer ear, respectively (Fig. 2). It can be assumed that these SPL ratios are used to decode partial sounds at higher levels of the dolphin's auditory system.

Based on the morphology similarity of Odontoceti, it is natural to suppose that their MFs and the morphological structures of the rostrum and skull play the role of external ears and form signs of spatial localization of sounds.

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CONFLICT OF INTEREST

The author declares that he has no conflicts of interest.

REFERENCES

1. D. L. Renaud and A. N. Popper, *J. Exp. Biol.* **63**, 569 (1975).
2. L. D. Korolev, N. V. Lipatov, R. N. Rezvov, M. A. Savel'ev, and A. B. Flenov, in *Proc. 8th All-Union Acoustical Conf.* (Moscow, 1973), Vol. 1, p. 125.
3. B. K. Branstetter, S. J. Mevissen, L. M. Herman, et al., *Bioacoustics*, No. **14**, 15 (2003).
4. J. A. Simmons, S. A. Kick, B. D. Lawrence, C. Hale, C. Bard, and B. Escudie, *J. Comp. Physiol.* **153**, 321 (1983).
5. J. Blauert, *Spatial Hearing: the Psychophysics of Human Sound Localization* (MIT Press, Cambridge, MA, 1997).
6. R. M. Warren, *Auditory Perception: a New Analysis and Synthesis* (Cambridge Univ. Press, Cambridge, 1999).
7. R. A. Butler, R. A. Humanski, and A. D. Musicant, *Perception* **19**, 241 (1990).
8. M. B. Gardner, *J. Acoust. Soc. Am.* **54** (6), 1489 (1973).
9. R. A. Butler, in *Handbook of Sensory Physiology* (Springer-Verlag, Berlin, 1975), Vol. 5(2), p. 247.
10. I. A. Gorlinsky and A. I. Konstantinov, in *Proc. 4th Int. Bat Research Conf.* (Nairobi, 1978), p. 145.
11. R. A. Norberg, *Phil. Trans. R. Soc. London Ser. B* **280**, 375 (1977).
12. E. I. Knudsen and M. Konishi, *J. Comp. Physiol. A* **133**, 13 (1979).

13. D. R. Ketten, *IEEE. Proc. Underwater Acoust.* **1**, 264 (1994).
14. W. W. L. Au and P. W. B. Moore, *J. Acoust. Soc. Am.* **75** (1), 255 (1984).
15. E. V. Romanenko, *Acoust. Phys.* **65** (1), 103 (2019).
16. F. C. Fraser and P. E. Purves, *Bull. Brit. Mus. Nat. Hist., Zool.* **7** (1), 1 (1960).
17. K. S. Norris, in *Evolution and Environment*, Ed. by E. Drake (Yale Univ. Press, New Heaven, 1968), p. 297.
18. V. V. Popov, A. Ya. Supin, V. O. Klishin, et al., *J. Acoust. Soc. Am.* **123** (1), 552 (2008).
19. T. W. Cranford, P. Krysl, and J. A. Hildebrand, *Bioinspir. Biomimet.* **3**, 1 (2008).
20. V. A. Ryabov, *J. Acoust. Soc. Am.* **1144**, 2414 (2003).
21. V. A. Ryabov, in *Proc. 3rd Int. Conf. Marine Mammals of the Holarctic, Koktebel, Crimea, Oct. 11–17, 2004* (Moscow, 2004), p. 483.
22. V. A. Ryabov, *Nat. Sci.* **2** (6), 646 (2010).
<https://doi.org/10.4236/ns.2010.26081>
23. V. A. Ryabov, *Biophysics* **59** (3), 475 (2014).
24. V. A. Ryabov, *St. Petersburg Polytech. Univ. J.: Phys. Math.* **2**, 240 (2016).
<https://doi.org/10.1016/j.spjpm.2016.08.003>
25. G. B. Agarkov, B. G. Khomenko, and V. G. Khadzhinskii, *Dolphins Morphology* (Naukova dumka, Kiev, 1974) [in Russian].
26. C. Barroso, T. W. Cranford, and A. Berta, *J. Morphol.* **273** (9), 1021 (2012).
<https://doi.org/10.1002/jmor.20040>
27. U. Varanasi and D. C. Malins, *Biochim. Biophys. Acta* **231**, 415 (1971).
28. D. R. Ketten, *The Biology of Hearing*, Ed. by D. Webster, R. Fay, and A. Popper (Springer-Verlag, New York, 1992), Vol. 13, No. 2, p. 43.
29. S. H. Ridgway and W. W. L. Au, *Encyclopedia of Neuroscience* (Elsevier, Madrid, 2009), **Vol. 4**, p. 1031.
<https://doi.org/10.1016/B978-008045046-9.00263-1>
30. W. W. L. Au, *The Sonar of Dolphins* (Springer-Verlag, New York, 1993).
31. P. W. B. Moore, D. A. Pawloski, and L. A. Dankiewicz, in *Sensory Systems of Aquatic Mammals*, Ed. by R. A. Kastelein, J. A. Thomas, and P. E. Nachtigall (De Spil, Woerden, 1995), p. 11.
32. M. P. Ivanov, S. N. Butov, L. E. Leonova, E. V. Romanovskaya, and V. E. Stefanov, *Acoust. Phys.* **65** (5), 603 (2019).
33. K. A. Rossbach and D. L. Herzing, *Mar. Mammal Sci.* **13**, 498 (1997).
34. V. E. Pyatetskii and V. M. Shakalo, *Bionika* **9**, 46 (1975).
35. E. V. Romanenko and E. G. Yanov, in *Marine Mammals. Research Results* (Nauka, Moscow, 1978), p. 241 [in Russian].

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