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Comparative Analysis of Spatial Hearing of Terrestrial, Semiaquatic and Aquatic Mammals

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1. Introduction

The comparative analysis of own experimental researches of accuracy and mechanisms of orientation in acoustic space of the Black Sea bottlenose dolphins, north fur seals and dogs were accomplished depending on parameters and environment of sound distribution. From all of the probed representatives of marine mammals dolphins differ the most exact indexes of sound source localization (1.5-2º). Fur seals localization possibilities in water are substantially less to such the dolphins in 1.6-1.8 time in a horizontal plane and in 5-9 times, sometimes more in a vertical plane. The accuracy of localization of sound source by fur seals in a horizontal plane in air (3.5-5.5º) a few exceeds such in water (6.7-7.5º) and appeared substantially better, than for dogs (7-11º), but in 1.5-2 times worse, than in water in a vertical plane . The mechanisms of acoustic orientation depend on the type of animal, his ecology, parameters, conducting path, sound path environment, features of sound path structures. For all speeches the direction of acoustic signal arrival encoding is carried out by means of space-frequency filtration and interaural differences.

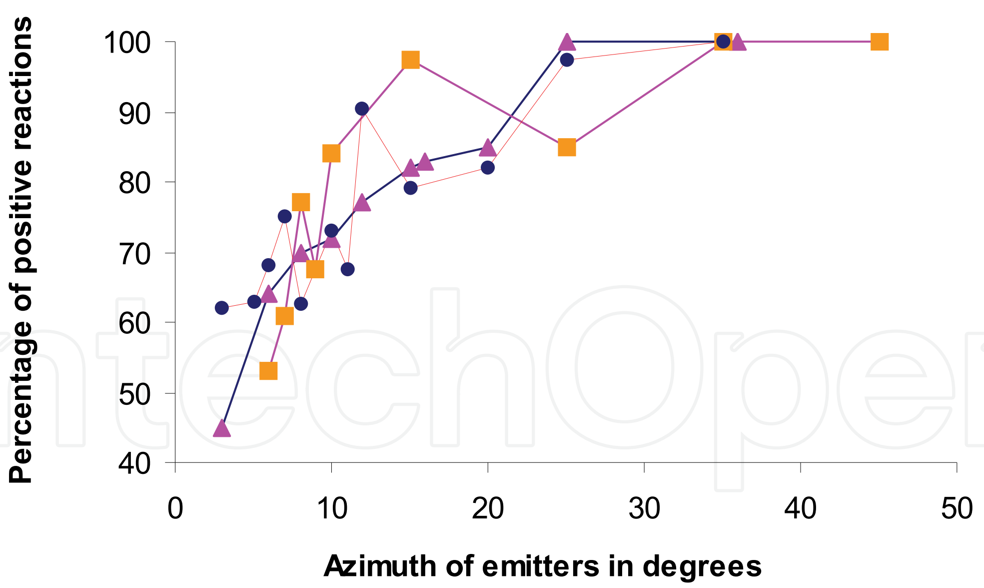
Peculiarities, accuracy and mechanisms of acoustic orientation of high level progress animals are investigated during many years by different authors using various methods. We have been already working on this theme over 30 years, in particular carrying out experimental researches (using behavioral response techniques operant conditioning with food reinforcement) of main characteristics of hearing, including space hearing, of aquatic and semiaquatic mammals – bottlenose dolphins and pinnipeds - big-eared and real seals (northern sea fur-seal and Caspian seals). The results of our researches and survey of summary of other authors' works are cited in our articles (Babushina, 1979, 1997, 1998, 1999, 2000, 2001 a, b, c; Babushina et al., 1991; Babushina & Polyakov, 2001, 2003, 2004; Babushina & Yurkevich, 1994 a, b; and others). All investigated mammals' representatives showed excellent abilities to take their bearings in space by means of hearing: to discover successfully acoustic signals, with high enough accuracy (but for every species – with its own one) to determine the place of the sound source, to define operating factors of signals, delicate structure of composite sounds, to use all functional possibilities of acoustic analyzer for solution of complicated experimental problems. Perhaps, at first it was a success for us to carry out multi-aspect, complex researches of peculiarities and mechanisms of mammals' acoustic orientation with different adaptive modifications of peripheral structures of hearing organ. It was determined, that main physical principles of sound source localization, using

by a man, are just applied for other mammals according to anatomic, morpho-functional peculiarities of a concrete specie, its ecology.
In this work the range of investigated mammals is extended – the data of localization accuracy of the acoustic signals source by three dogs in the horizontal plane which we obtained are cited at first. The results are discussed in comparison with carried out analogical researches of dolphins and pinnipeds.
Localization of tonal signals source by dogs. The information about functional characteristics of acoustic analyzer of family doggy representatives are not numerous (Gorlinskiy & Babushina, 1985; Kalmykova, 1977; Goldberg & Brown, 1969; Issley & Gysel, 1975; Peterson et al., 1966, 1969). By the average data (on seven mammals) (Peterson et al., 1969) the range of dog's hearing is stretched from sound frequencies to 60 kHz with area of high sensitivity from 0.2 to 15 kHz. The most microphone potential was registered in uniform in magnitude response of area from 0.25 to 7 kHz.
At I. V. Kalmykova's work (Kalmykova, 1977) on dogs using the method of defensive conditioned reflexes lateralization of sound image was investigated in dichotic presentation of a series of clicks for the two signal levels – 60 and 20 dB above standard sound pressure level. Interaural minimum discernible differences in the intensity and time were found to be 2.2 dB and 75 ms, i.e. much higher than similar values for humans.
Investigation of localization abilities of dogs (mongrel, with erect ear shells) was carried out by the method of instrumental conditional reflexes with food reinforcement.
The dogs have elaborated a conditioned reflex to hold the original position, touching the tip of its nose, one of three (central) manipulator - rubber ball suspended at some distance from a line parallel to the plane of the emitters.
The distance from the middle base between acoustic meatuses to the plane of emitters location was at a frequency of 4 kHz, 1 m, at higher frequencies – 0.5 m. Head position at which both ears were in a plane parallel to the arrangement of the emitters at the same distance from central manipulator, was taken conformity with relevant zero azimuth. Two emitters were mounted at the height of acoustic meatuses of dogs at the same distance from the 0^o-azimuth plane. During the experiment, the angle of signal arrival relative to the zero azimuth direction could vary from 45 to 3^o. In the experiments, the signal was fed by alternately one of emitters in a random order. Animals were trained to touch with a paw the left or the right manipulator according to the direction of sound arrival. Each adequate reaction of the animal was accompanied by food reinforcement.
To study the limits of dogs localization abilities the azimuth of emitters decreased in increments of 10^o from 45 to 15^o and increments 5-1^o of 15^o or less. An indicator of the dogs localization limit ability was the minimum detectable angle (MDA), equal to the azimuth of the emitter, corresponding to 75% level of positive reactions.
The limit values for azimuth localization by dogs of tone source parcels were measured for frequencies 4, 10 and 30 kHz. The choice of frequencies 4 and 30 kHz was due to their correspondence to tonal stimuli, which were presented in experiments with dolphins in the air environment (Babushina, 1979). The frequency 10 kHz was chosen as intermediate between two above signals. Rise time of the amplitude of tone parcels frequency 4 and 10 kHz was 20 ms, decay time – 25 ms. For signal with frequency 30 kHz corresponding values were within 20 mks. The duration of signals was 1 s.
The sound pressure level in the initial position of the animal reached 75, 88 and 65 dB (relative to 0.0002 dyn/cm^2) at frequencies of 4, 10 and 30 kHz, accordingly.

The work was done using standard radio measuring equipment. The experiments were performed on three dogs.

4 kHz			10 kHz			30 kHz		
α°	**n**	**P(%)**	**α°**	**n**	**P(%)**	**α°**	**n**	**P(%)**
3	107	61 ± 5.6	3	20	45 ± 1.3	6	36	53 ± 6.2
5	42	62 ± 8	6	76	64 ± 3.9	7	31	61 ± 14
6	188	68 ± 3.9	8	107	70 ± 8.9	8	53	77 ± 12
7	107	75 ± 8.2	10	136	71 ± 2	9	95	67 ± 2
8	101	63 ± 7	12	52	77 ± 11	10	63	84 ± 0.1
9	147	67 ± 3.1	15	149	82 ± 2.7	15	38	97 ± 2.5
10	474	73 ± 4	16	30	83 ± 6.2	25	88	83 ± 8
11	21	67 ± 8.7	20	37	84 ± 12	35	20	100
12	31	90 ± 9.7	25	10	100	45	20	100
15	258	79 ± 3.4	36	30	100			
20	54	81 ± 10.6	45	30	100			
25	67	97 ± 2.8						
35	38	100						
45	244	100						

Table 1. Localization of tonal signals source by dogs in the horizontal plane (averaged data). Symbols: α°– the azimuth of emitters; n – the number of tests; P (%) – - the percentage of positive reactions.



Pic. 1. The dependence of the percentage of positive reactions (P %) of dogs on the azimuth (α°) of tonal signals sources (averaged data).
Symbols: circles – 4 kHz, triangles – 10 kHz, squares – 30 kHz

Averaged results of experiments are presented in the table 1 and on figure 1. For signals with frequency of 4 and 10 kHz the data were averaged for three dogs, for the signal with frequency of 30 kHz - in two animals, as one dog in further experiments did not participate. The data show that with decreasing of sources azimuth the share of positive reactions of animals decreases. Sustainable dependence of the percentage of positive reactions from the frequency of the signal at each given value of the azimuth emitters was not found. In pic. 1 one can see that the curves are close to one another. For frequencies 4 and 30 kHz there is a double crossing of the curves with the threshold level. Defined graphically the minimum detectable azimuth of emitters by animals was within the limits of 7-11° for the signal with frequency 4 kHz, 11° for the stimulus 10 kHz, 8-9.5° 0 for the signal with frequency 30 kHz, i.e. localization indices for the investigated monofrequency signals were similar.

Thus, the maximum perceived by dogs change of tone source azimuth in the frequency range 4-30 kHz (at the level of 75% of positive reactions) is not less than 7°.

Apparently, in the investigated frequency range the dogs oriented mainly on binaural differences in intensity of the stimulus. Similar values of limiting angles of localization obtained for different frequencies in our experiments with dogs suggest equal efficiency of binaural differences in intensity in all investigated frequencies (4-30 kHz).

Measuring of periferal hearing orientation in dogs (Gorlinskiy & Babushina, 1985) showed that with increase of frequency and the angle of the sound arrival the tendency to the growth of interaul differences is watched in the intensity of sound (Δ I), that increase efficiency of using Δ I in mechanism of source signal localization. The focus of auditory reception in dogs is provided at frequencies 0.5 and 1 kHz by acoustic properties of the animal's head, and over 1 kHz - spatial-frequency selective of external ear.

These experiments have allowed to understand the mechanisms which ensure a successful sound orientation, and revealed a crucial role towards the properties of ears in space hearing of terrestrial animals. The received material in conjunction with the analysis of other authors data suggests that the peripheral structures of the dogs auditory analyzer, like all mammals, not only terrestrial but also aquatic, decode acoustic space on the principle of directional frequency filtration. Of particular significance for the detection and localization of a sound source by dogs has the mobility of ears. In mid and high frequency ranges of sounds the turn of auricle influenced on the position of the maxima and the shape of the directivity patterns of reception. After the motor component of the orienting reaction the animal's head is turned to the sound source. Observed with the movement of auricles in a frontal position transfers maxima diagrams admission closer to the midline of a head. Steepening of the diagrams in this area along with some narrowing of focus, as well as increasing near the midline dog's head of a strictly monotonic function Δ I from the angle of sound arrival provide some optimization of processing acoustic information.

The values of the minimum perceptible by our experimental dogs azimuth of monofrequency signals source (7-11° in the researched frequencies range) are in good agreement with the results of experiments with dichotic presentation of the sound stimulus (Kalmykova, 1977). The 75% level of positive reactions in these experiments corresponded to binaural time differences equal to 75 microseconds, and the binaural difference in the intensity of 2.2 dB. As you can see, these values are significantly higher than the minimum values of Δ T (10 ms) and Δ I (0.5 dB) for a human obtained at a frequency 0.75 kHz (Casseday & Neff, 1973). At the same time binaural ΔT andΔ I for dogs compared with the corresponding values for the monkeys (60-180 ms and 6-10 dB, with 85% level of positive reactions) (Don & Starr, 1972) and slightly higher than the data for the cat (20 - 50 ms) (Masterton & Diamond, 1964; Masterton et al., 1967, 1968). In all experimental dogs interaural distance was in the range 9.5-11 cm. In such basis the binaural differences in arrival time or phase of the signal become effective at a frequency of less than 1.7 kHz (the sound wavelength of more than double interaural distance), and only at a frequency 3.3 kHz the wavelength is comparable to the base (an average of 10.2 cm for the experimental dogs). For a human such a transition zone corresponds to the frequency 1.7 kHz, for the cat - 4 kHz.

Consequently, at a frequency of 4 kHz and above dogs were able to focus on the binaural difference in stimulus intensity, which probably took place. Somewhat smaller accuracy of localization of tonal sounds source by cats in the range of 2-8 kHz (Casseday & Neff, 1973) due, apparently, the size of the head, and consequently, less interaural distance, compared with dogs. High resolution of human auditory analyzer (1.5°) (Mills, 1958) at a frequency of 4 kHz to some extent also due to the size of the base.

High accuracy of definition of the ultrasound source direction (less than 1°) was found at bats (Gorlinsky, 1975, 1976). Based on the analysis of directional diagrams of receiving of ears of sharp-eared bats and the Greater Horseshoe Bat, as well as the results of localization experiments, the author concludes that neither the time nor phase binaural mechanisms can cannot explain such high localization ability of the animals. Only the assumption that the threshold of perception of interaural differences n the intensity in bats, like other mammals, does not exceed 1 dB, could satisfactorily explain the obtained data.

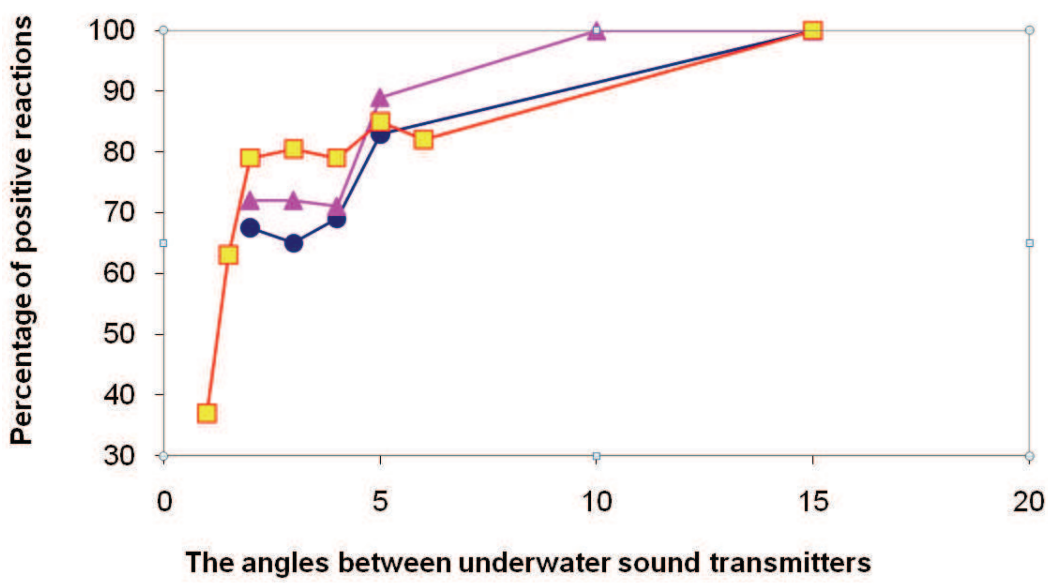
5 kHz			**20 kHz**			**120 kHz**		
α°	**n**	**P(%)**	**α°**	**n**	**P(%)**	**α°**	**n**	**P(%)**
2	241	68 ± 5.9	2	278	73 ± 6.1	1	8	37 ± 12
3	204	66 ± 6.1	3	200	73 ± 4.9	1.5	70	64 ± 6
4	66	70 ± 1.2	4	312	72 ± 5	2	462	80 ± 2.5
5	205	83 ± 1.2	5	206	89 ± 6.1	3	247	81 ± 4.7
45	30	100	10	20	100	4	76	80 ± 5
			45	30	100	5	35	85 ± 1.2
						6	400	83 ± 3.7
						15	20	100
						25	60	100
						35	60	100
						45	176	100

Table 2. Localization of tonal signals source by dolphins in the horizontal plane (averaged data). Symbols: α° – the angles between underwater sound transmitters; n – the number of tests; P (%) – - the percentage of positive reactions.

The dependence of correct responses percentage of two bottlenose dolphins on the angle between underwater sound transmitters for tonal signals is shown in the figure 2 and in the table 2 (Data on Babushina, 1979) for the comparison with the same values for the dogs (fig. 1 and table 1).

It was found by the experiment that animals which live in the water and have a rich set of adaptations of the specialized auditory analyzer (respectively ecology of concrete species), are able to orient successfully in an acoustic space, determine the direction on the sound source. To be efficient under water, the organ of hearing must be sensitive and capable of binaural analysis. In addition, the resonance frequency of the mechanical vibration system of the middle ear must be shifted under water (relative to that in air) to allow ultrasound

reception. The hearing system of aquatic and semiaquatic mammals possesses all these properties (Lipatov, 1978).
The good indexes of directional hearing in the water and in the air (in this environment - even better than dogs have) are found in different species of pinnipeds (Babushina, 1998; Babushina & Polyakov, 2004; Babushina & Yurkevich, 1994 a; Gentry, 1967; Moore, 1975; Möhl, 1964; Terhune, 1974). Let us draw attention on our own studies of northern fur seal space hearing.



Pic. 2. The dependence of the percentage of positive reactions (P %) of two dolphins on the angles between underwater sound transmitters for tonal signals sources(averaged data). (Data on Babushina, 1979).
Symbols: circles – 5 kHz, triangles – 20 kHz, squares – 120 kHz.

Using the method of instrumental conditioned reflexes technique with food reinforcement, we investigated the accuracy of localization by northern fur seals of different sources of acoustic signals in the horizontal plane in the water and air environments (Fig. 2,3) (Babushina & Polyakov, 2004). Threshold limit values of angles were estimated (in all our experiments) on the level of 75% of positive reactions. In the frequency range 0.5-25 kHz the accuracy of localization by fur seals tone source pulses (duration 3-90 ms) is in the water 6.5-7.5^{o}, in the air (for duration of the pulse 3-160 ms) - 3, 5-5,5^{o} (better than dogs have). The source of noise pulses (bandwidth 1-20 kHz, duration 3 ms) is localized by fur seals in the water with accuracy 3^{o}, continuous (duration 1 s), narrow-band (10% of the central frequency) and broadband (bandwidth 1-20 kHz) noises in the air - with an accuracy of 2-5^{o} 0 and 4.5^{o}, respectively. The data obtained allow to conclude that the signs used by fur seals in the localization of tonal pulses are likely to be equally effective for different frequencies (at least in the investigated frequency range). The source of broadband noise pulses, carrying a few signs of binaural localization, bears by seals at greater accuracy than a source of tonal pulses. Contrary to expectations, the significant increase of accuracy of localization in the air (as compared with the results for water) - about five times, according to the theory of binaural hearing, due to the decrease of sound velocity and, consequently, the increase of binaural time differences - not observed. Perhaps this is due to the change of the system resonances and transmission characteristics of the seal's external ear, slightly open in the air. In addition, the ears of the seal rolled into a tube and are oriented front to back, which also is not conducive to the directional auditory reception in the air.

A significant contribution to the study of space hearing is the study of localization capabilities of the animal in the vertical plane. According to our data (Babushina & Yurkevich, 1994 a), the accuracy of determine by fur seals the direction of arrival sound in the vertical plane in the water depends on the parameters of acoustic signals and amounts (peak angle, i.e. the angle between the upper and lower emitters at zero azimuth): 7-8° - for clicks (representing the reaction of the emitter to rectangular pulses of 0.5 ms and 1 ms), broadband noises (bandwidth 0.5-20 kHz), narrowband (10% of the central frequency) noise pulses with center frequencies 2-4 kHz, 12-20°- for continuous narrowband noises and noise pulses with central frequencies 5-20 kHz; 18 -20° - for tonal pulses with smooth fronts of amplitude variation.

The results showed that the accuracy of localization by fur seals of the source of acoustic signals in the vertical plane in the aquatic environment depends on their parameters such as in humans rises for the sounds with a complex spectra and is probably substantially reduced due to the presence of reverberation noise, especially for tonal pulses of long duration and high pulse repetition rates. Considerable difficulties which fur seals have (like humans) at localization in the vertical plane of monofrequency sounds source, due, apparently, and the absence of signals have to be, at least three frequency components (as shown in studies in humans and some terrestrial animals) with a certain ratio of the amplitudes. The deterioration of seal's localization abilities vertically with increasing center frequency of narrowband noise pulses is difficult to explain - in pinnipeds underwater sound reception provided the full range of conductive structures, the specific role of each of which encode the vertical coordinates of the source is still unclear.

The accuracy of localization by fur seals of the source sound vertically in the air at nonzero values of the emitters azimuth (27° -35°) is (peak angle): 14.5° and 21°, respectively, for broadband and narrowband (with a center frequency of 5 kHz) noise pulses (Babushina, 1998). The source of narrowband noise pulses with center frequencies 2, 4, 10 kHz is localized by seal at the level of random selection (with the angles between the emitters - 22-30°).

It turned out that in the air the direction to the sound source in the medial (with zero values of the emitters azimuth) vertical plane, and at azimuth 90° the seal cannot define. The reason probably lies in the simple structure of the auricle seal which is devoid of typical for a human of many folds and ledges, which create for different angles the elevations of the sound source the complex combination of the diffraction pattern, interference, scattering, rounding, the resonances which significantly improve the accuracy of localization by a human the sound source in the vertical plane. In addition, the tubular shape of the seal auricle and its specific orientation (front to back) is also not conducive to the orientations of the auditory reception.

Perhaps some of these factors explain the inability of fur seals to locate the source of even complex sounds in the medial vertical plane in the air. At zero emitters azimuth variation with the change of frequency and angle of elevation caused by tissues of the head are minimal but increases with nonzero values of the azimuth (Searle et. al., 1975), which probably contributes to the determination of northern fur seal in the direction of the sound source in the vertical plane at non-zero azimuths emitters. However, it comes with a noticeably less success than in humans (Altman, 1983, Altman et al, 1990). Perhaps the seal as a human also uses the additional binaural cues localization vertically through the light asymmetry of the ears.

These data indicate that the seal's ability to determine the direction to sound source in a vertical plane in the air depends on the parameters of acoustic signals, as well as in humans, rises for the sounds of complex spectra (containing much information about the coordinates of the sound source) and 1.5-2 times worse than in the water (which can be partly attributed to the different seal conductive channels in the water and in the air).

Localization opportunities and mechanisms of the dolphins directional hearing have been studied by many authors (Akopian et al., 1977; Bel'kovich & Dubrovsky, 1976; Bel'kovich & Solntseva, 1970; Voronov, 1978; Dyachenko et al., 1971; Zaitseva, 1978; Zaitseva et al., 1975; Ivanenko & Chilingiris, 1973, 1978, Korolev et al., 1973; Andersen, 1970; Dudok van Heel, 1959; Renaud & Popper, 1975 and others). Dolphins have several channels of sound conduction and this availability makes it difficult to study the mechanisms of space hearing in these mammals. Detailed review of works that have examined the features of sound conduction in marine mammals, is given in the article (Babushina, 2001). Auditory channal and the lower jaw which dolphin has in the aggregate with their surrounding tissues to a large extent form the direction of auditory reception (Purves & Utrecht, 1964). It was proved that in the formation of directional reception by dolphins of high frequency signals can take part different entities of soft and bone tissues, such as hypodermis of the lower jaw (Ravens, 1978; Stosman & Voronov, 1978; Stosman et al., 1978). Scanning movements of the head contribute to more precise analysis of the differences in the intensity and spectral pattern on the two receivers (Bel'kovich & Solntseva, 1970). Complex sounds, we can say "fall apart" by the conductive channels, interact with them, changing, creating a specific spectral pattern in the auditory centers, depending on the coordinates sound source.

Let us dwell on our own studies of space hearing of the Black Sea bottlenose dolphin

Tursiops truncatus p.

According to our data (Babushina, 1979), the limit angles of the localization by two bottlenose dolphins the source of acoustic signals in the horizontal plane in the water are as follows: for tonal pulses in duration of 1 s, frequency of 5, 20 and 120 kHz, respectively, 4,5, 4^{o} and less than 2^{o}, for pulses whose parameters vary within the limits of variability of echolocation
signals – $1.5\text{-}2^{o}$.

Investigation of limiting localization capabilities of bottlenose dolphins in the vertical plane showed high resolution of the auditory analyzer for both the tone and for pulsed signals (Babushina & Polyakov, 2008). The minimum detectable angle for the tone frequency of 5 and 20 kHz was within 2.5^{o}. The magnitude of the limit angle for the stimulus frequency of 120 kHz was 2^{o}, i.e. coincided with that for the horizontal plane. The maximum angle of localization of pulse click sequences (with a maximum energy at a frequency of 120 kHz, the duration of the pulses 20 ms, repetition rate 300 Hz) in the vertical plane was little more than 1.5^{o}.

Changing of the intensity of the received stimuli spectrum with the change of place angle, perhaps, reports to the dolphin the primary key for sound localization in the vertical plane. Characteristics of conditioned reflex reactions generated by the dolphin do not preclude the possible movements of the head at the time of presentation of the signal. So, perhaps, the dolphin used the binaural-added information (both in the time and intensity) to determine of sound source position. Dolphin, carrying out scanning reception by turning the head, can change the characteristics of its receiving filters, matching them with the test signals, and thus fulfill the optimal space-frequency filtering (Ayrapet'yants and others, 1973). Comparable values of limit localization angles of monofrequency source of acoustic signals by our dolphin in the vertical plane give rise to assume the existence of different, in a similar degree the effective cues for localization at different frequencies. This is consistent with data obtained by us in the localization of the various sounds by dolphins in the horizontal plane (Babushina, 1979), and with the results and hypotheses of localization mechanisms of other authors (Terhune, 1974; Moore, 1975; Renaud & Popper, 1975).

The results of our research of localization capabilities of the Black Sea bottlenose dolphins (*Tursiops truncatus p.*) in the horizontal and vertical planes are in very good agreement with experimental data Renaud D. and A. Popper (Renaud & Popper, 1975) obtained for Atlantic bottlenose dolphin (*Tursiops truncatus*). This is all the more interesting that, unlike our experiments, in the above-mentioned authors' work the animal's head was fixed. In addition, the localization in the vertical plane was investigated at the location of a dolphin on his side. As in our experiments, in the work (Renaud & Popper, 1975) it was investigated the accuracy of localization over a wide frequency range (6-100 kHz) for tonal signals and sequences of clicks with an energy spectrum similar to that of echolocation pulses of dolphins. There was no significant difference in the accuracy of localization in the horizontal and vertical planes. Thus, at frequencies of 30, 60 and 90 kHz limit vertical localization angles were, respectively, 2.5º, 3º and 3º. In this work the limit localization angles of the clicks sequences (with the parameters, similar to those of sonar signals) were 0.7 and 0.9º, respectively, in the vertical and horizontal planes. Based on the data obtained and the results of other researchers (Bullock et. al., 1968; McCormick et. al., 1970; Norris & Harvey, 1974) the authors suggested that at low frequencies the sound localization is carried out by the meatus, at frequencies around 20 kHz and above - through the lower jaw and, at frequencies above 20 kHz, the animals are guided by binaural differences in signals intensity. At the vertical localization the dolphin's low jaw was focused on one emitter, and the top - on the other one. In the experiments in the vertical plane (Renaud & Popper, 1975) the dolphin could not use binaural information as his head at the time of the signals supply was fixed. T. Bullock with co-authors (Bullock et.al, 1968) showed that the sounds coming through the jaw, cause in the lower colliculus midbrain responses greater magnitude than the sounds that pass through the dorsal part of the rostrum. These differences could be used by dolphin, believed to J. Renaud and A. Popper. Free animal (with movable head, as in our experiments) can, moreover, determine the vertical coordinates of the sound source by remembering on the short time parameters of the signals and comparing them with the characteristics of sounds in the other head position (Renaud & Popper, 1975).

Dolphins' localization abilities what we investigated exceed similar capabilities of semiaquatic animals - pinnipeds, especially in the vertical plane (when compared to the optimum for each frequency bands) (Babushina, 1998; Babushina & Polyakov, 2004; Babushina & Yurkevich, 1994 a). So, the best indicator of the "horizontal" localization by fur seals of broadband noise pulses (3º) is in 1.6-1.8 times less than localization abilities of a dolphin, measured in the horizontal plane at high frequencies (50-120 kHz), short pulses - 1-1.9º. In the vertical plane, similar differences increase substantially - the accuracy of localization by fur seals of tone source and a variety of complex sounds vertically in the water (Babushina & Yurkevich, 1994 a) in 5-9, sometimes more than once is inferior of localization dolphin's opportunities. Obviously, successful vertical localization requires a certain set of high-frequency components of the spectrum. Naturally, with such a task only complex dolphin auditory analyzer could easily handle, to a large extent formed by the evolution of echolocation function. One reason for the above differences in terms of space hearing, undoubtedly due to anatomical and functional differences in the dolphins' conductive structure and pinnipeds. In details it is outlined about conductive structures of pinnipeds in the work (Babushina & Yurkevich, 1994 a), showing all the major studies on this topic. Clearly, a large role in the auditory orientation belongs to the functional characteristics of the central sections of hearing organ of marine mammals.

For further study of the mechanisms of dolphins' directed auditory reception, as well as for comparison with terrestrial mammals from which they descended, we measured the accuracy of localization of acoustic signals by dolphins in the air (Babushina, 1979). According to our data (Babushina, 1986), the range of perception by dolphin of acoustic signals in the air ranges from 1 to 110 kHz with the greatest sensitivity to low frequencies (1-40 kHz). The lowest auditory thresholds ware recorded on frequency of 40 kHz (-44 dB relative. 1mkb). Dolphin worse hears the air sounds at 10-13 dB, when its alveary immersed in the water, compared with thresholds in the case when the whole head is in the air. The comparison of aerial and underwater audiograms of a bottlenose dolphin in the coordinates "intensity-frequency" has shown that the sensitivity of the dolphin's ear to the sounds in the air worsens by 30-60 dB (depending on frequency). For comparison (Babushina, 1997; Babushina et al., 1991): hearing sensitivity of pinnipeds to the underwater sounds at 15-20 dB exceeds the sensitivity in the air and only in 7-15 dB is inferior to that of dolphins in comparison at the best frequencies (for each species) of auditory perception. Northern fur seal hears in the water as good as the humans in the air; the sensitivity of hearing of seals to underwater sounds only in 7-10 dB below than the sensitivity of human hearing in the air. Comparing the curves of our dolphin hearing in the air and a human underwater in the frequency range of 0.125-8 kHz (Hollien & Brandt, 1969), we can say that the dolphin in the air at low frequencies hears much better than people in the water. From 0.125 to 2 kHz thresholds of human hearing in the water are equally high (about 70 dB relative to 0.0002 mcB) and up to 8 kHz is further increas by 12.5 dB. The difference between thresholds in two environments for a human at frequencies 0.25, 1 and 2 kHz is about 29 and 51 and 59 dB (relative to 0.0002 mcB), respectively.

As shown by studies of many authors, a human hears under water, mostly through bone conduction. In this paper, using the contact stimulation by tonal signals at the frequencies of 1 and 30 kHz it was showed that the thresholds corresponding to the bone structures and soft tissues of the human head differ only slightly (Soluha, 1973). On this basis, it was hypothesized that in aquatic environment sound conduction is realized by tissue structures - a distributed receiver about the size of 0.2 m. Researchers related the ability of the human organ of hearing to detect the direction of underwater sound signals and to locate their source mainly to the sound-conducting properties of the tympanic structures and to a lesser extent to bone conduction (Hollien, 1973 and others). However, not all phenomena could be explained. There were studies that reported the involvement of human skin in locating the source of underwater sound. For example, in Hollien's experiments (Hollien, 1973), human skin was found to possess sound-conducting properties: the subjects could sense underwater sound signals with foot, hand, or face skin.

Through mathematical calculations it was showed that human's hearing thresholds under water, at least, on sound frequency are defined as in the air by the passage of acoustic vibrations through external auditory channel (Lipatov, 1978).

There is evidence that people under water localize the sound source not worse than a dolphin in the air (as shown below), and almost in the same extent as semiaquatic mammals in the water. The literature cites a number of experimental data about fairly successful, especially at low frequencies, the localization by a human under the water of low frequency sound sources and broadband signals - 7-11° after exercise (Feinstein, 1973; Hollien, 1973). The authors suggest that binaural time differences are most informative for human and in underwater sound localization at low frequencies. Localization of the sound source under water can be provided by a number of mechanisms, as usual for the man - the air, and additional, caused by aquatic environment.

It turned out that in the air in a horizontal plane the source as of tone (4.5 and 28 kHz) and as pulse (with a carrier frequency of 20 kHz) signals is localized by a dolphin with the same accuracy consistent with the limit angle between the emitters of the order 20-21°.

By investigating the limits of localization capabilities of dolphins in the air (Babushina, 1979) the frequency of tonal stimuli was chosen on the basis of equality of the wavelength of tones in the air and water. Consequently, the sizes of the base (distance between the host signal structures) for each wavelength were identical in two environments. For pulsed stimulus temporal binaural differences are also the only factor, mixed in the water, and air. Thus, the localization conditions differ only in the speed of sound. Since the air has an advantage for the localization on the time parameter, it could be expected increase of accuracy of localization in this environment, similarly to the tests on the seals. However, experiments have shown the deterioration of the localization ability of a dolphin in the air, both for tone and for the pulse signals at about 10 times, compared with those for water. However, the obtained values of the limit localization angle by a dolphin the sound in the air is about 2 times differed from the corresponding minimum of values of the angle, as shown by dogs.

A dolphin has two independent acoustic receivers, as well as several sound-transmitting channels, due to complete isolation of the hearing organ from the vibration of skull bones it could be expected the best localization indexes in the air. The question is through what binaural mechanisms dolphins localize the source sound in the air, is still controversial. In the air at a frequency of 4.5 kHz is probably a manifestation of the shielding effect, certainly, in different extent with different possible dolphin's bases. So there is a reason to believe that binaural differences in intensity at two ears ware in our experiments the most informative. Concerning pathways of sound to the dolphin's ear in the air and their weight fraction in sound localization presently uniquely it is difficult to say.

Conclusion. The study of limit localization abilities of a human and animals so far showed that from the terrestrial nonecholocational mammals human auditory analyzer has the highest resolution on the angle of the arrival of low-frequency sound. Echolocational mammals, both terrestrial and marine, through a highly specialized auditory system with high accuracy can determine the direction of the ultrasound source. The principles of sound localization in space, first formulated for humans, are apparently applicable to other mammals. Animals studies have confirmed and even more showed significant role of external structures of the hearing organ in sound localization. As a result of experiments on individual representatives of terrestrial, semiaquatic and aquatic mammals proved that the external structure of the auditory system are actively transforming the audio stream, creating a sharp focus of the reception of acoustic oscillations. Thus, initiated the study of specific mechanisms of peripheral auditory analysis of acoustic space.

It is experimentally proved that the auditory system of mammals is an environmentally adapted, the perfect device to ensure the success orientation in space.

The results of experiments on dolphins, namely, comparable values of the limit angle of localization in the water of source of various signals in both the horizontal and vertical planes, the independence of accuracy of acoustic localization from change (in the studied range) parameters of pulse signals give rise to assume the existence of different, in a similar degree of effective binaural cues for localization at different frequencies.

Similar values of the limiting localization angle of source signals of different frequencies in the air allow the ability to save different localization cues and in this environment. Comparison of mammals' space-hearing in the unusual habitats for them showed that both terrestrial and aquatic mammals, possessing highly specialized, adapted to their own environment by the auditory system, can, however, to navigate rather successfully in the uncharacteristic acoustic spaces for them. Characteristically, the dolphin localizes the sound and ultrasound source in the air with an accuracy of about two times smaller to localization abilities of dogs. At the same time, space hearing of a man under water does not yield the same characteristics of the dolphin in the air. Indicators of space hearing of semiaquatic animals do not vary greatly in two environments.

Figuratively speaking, the evolution of disposition ordered equally rightly in the development and functional specialization of the auditory system, both terrestrial and aquatic mammals, providing them with some "margin", and dolphins, as secondary aquatic animals, some "balance" of the old features.

Nevertheless, a significant deterioration in hearing sensitivity of dolphins to ultrasound in a wide range of frequencies in the air, along with the deterioration of the order of 10 times of their limit of localization abilities, characterizes the habitat as the main factor determining the physiological capabilities of mammal.

As a result of experiments with pinnipeds it is showed that signals containing explicit temporal characteristics, and are localized much more successful than the signals that carry information only about the intensity or phase. Signs used by northern fur seals in the localization in the horizontal plane of tone pulses, probably (as in dolphin), are equally effective for a variety of frequencies. Source of complex sounds that carry a few signs of binaural localization, is bearing by seals at a higher accuracy than the source of tonal pulses. The accuracy of localization of fur seals source of acoustic signals in the vertical plane in the water and air depends on their parameters, as in humans and other animals, increases to sounds with complex spectra. Moreover, the vertical source of sound in the air is localized by fur seals in 1.5-2 times worse than in the water.

It was found that the air direction of the sound source in the medial (at zero values of azimuth emitters) vertical plane, as well as when an azimuth 90º seal cannot determine. Localization capabilities of a seal in aquatic environment substantially inferior to those of a dolphin in 1.6-1.8 times in the horizontal plane and 5-9, and sometimes more than once - in the vertical plane (when comparing the best rates in the optimum for each frequency ranges). Such differences in indexes of space-hearing explained as anatomical and functional differences of dolphins and pinnipeds conductive structures, as well as differences of characteristics of the central sections of hearing organ of marine mammals.

Of all investigated representatives of marine mammals, dolphins are distinguished by the most accurate analysis of the acoustic space.

Comparison of directional reception outside of the hearing of bats, dogs, dolphins and other animals revealed the presence of a single mechanism for all types of encoding mechanism of the direction of arrival of acoustic signals through space-frequency filtering and interaural differences. The nature of orientation of auditory reception of mammals is due to excitation by impact of environmental factors.

The similarity in the properties of sound-conducting structures in dolphins and pinnipeds viewed through different modes of acoustic information processing in these species opens new avenues for comparatively analyzing the mechanisms of hearing. The results of basic studies of hearing in animals capable of perfect assessment of their acoustic environments may be useful in solving various applied problems (Babushina, 2001 c).

We obtained the very interesting data on investigation of sound reception in marine mammals: effect of stimulus parameters end transmission pathways (Babushina, 2000).

Underwater audiograms of the northern fur seal *Callorhinus ursinus,* the Caspian seal *Pusa caspica,* and the Black Sea bottlenose dolphin *Tursiops truncatus* were determined in experiments with fully or partially submerged (head out of water) animals by the operant conditioning technique with food reinforcement. The partial submergence conditions (the pinnae isolated from the sound-transmitting medium) were used to assess the sound-conducting characteristics of marine mammals body tissues. In the Caspian seal, the detection thresholds for acoustic signals of different frequencies were also determined in the presence of broadband or narrowband noise maskers of varied center frequency. The effect of the masker depended on the medium (air or water) in which the signal and the masker propagated, and on the conditions of sound reception (pinnae under or above water). The aerial and underwater sound-conducting pathways were shown to be functionally interlinked in the Caspian seal. The masking effect of noise on its hearing depended on (I) whether the signal and the masker were aerial, conducted via the external ear; or underwater, conducted via the specialized structures of the head and via head and body tissues; (II) the sensitivities of the hearing system to the signal and the noise; and (III) the signal and noise spectra. The data obtained suggested that the seal body tissues like tissues of the bottlenose dolphin altered the amplitude and frequency characteristics of acoustic signals.

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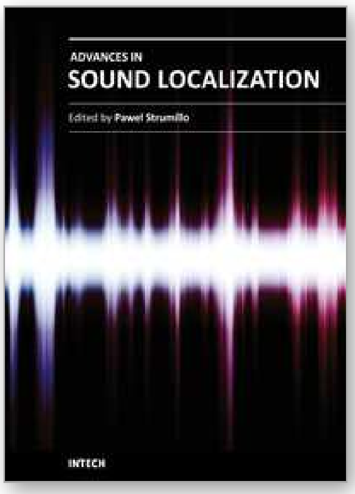

Advances in Sound Localization

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Sound source localization is an important research field that has attracted researchers' efforts from many technical and biomedical sciences. Sound source localization (SSL) is defined as the determination of the direction from a receiver, but also includes the distance from it. Because of the wave nature of sound propagation, phenomena such as refraction, diffraction, diffusion, reflection, reverberation and interference occur. The wide spectrum of sound frequencies that range from infrasounds through acoustic sounds to ultrasounds, also introduces difficulties, as different spectrum components have different penetration properties through the medium. Consequently, SSL is a complex computation problem and development of robust sound localization techniques calls for different approaches, including multisensor schemes, null-steering beamforming and time-difference arrival techniques. The book offers a rich source of valuable material on advances on SSL techniques and their applications that should appeal to researches representing diverse engineering and scientific disciplines.

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