

**N.G.Bibikov**  
**SOME PECULIARITIES OF ECHOLOCATING AUDITORY SYSTEM**  
**OF HARBOR PORPOISE**

N.N.Andreev Acoustics institute  
Russia, 117036 Moscow, Schvernika st.4  
Bodies: [499 7236311; the Fax: [495 1268411  
E-mail: bibikov@akin.ru

*General features of location acoustical signals and auditory system of a harbor dolphin (Phocoena phocoena) are analysed. It is specified, that high-frequency component of the location signal in this animal have been revealed by N.A.Dubrovsky with colleagues. The analysis of behavioural and various physiological data specifies that the harbor porpoise, possibly, possesses the most high-frequency hearing among animals in detail studied to the present time. Besides existence at this object acoustic "fovea" in area 130-140kHz comes to light. In the given frequency area not only the lowest thresholds of hearing are marked, but excellent frequency selectivity is revealed also. In the given area not only the lowest thresholds of hearing are observed, but excellent frequency selectivity is revealed also. The meaning of reactions to the termination of a signal, typical for this animal, is discussed in connection with possible specificity of the organization of the peripheral analysis on basilar membrane of the cochlea. The analysis of all received data allows to put forward a hypothesis that this animal could use precise time and frequency analysis of echo signal with the purpose of definition of speed of approaching with a source of echo signals.*

The sea pig, harbor porpoise or Azov dolphins (*Phocoena phocoena relicta* Abel, 1905) is the smallest dolphin in Russian aquatorium. The animal is widespread almost in all moderated and warm areas of world ocean in northern hemisphere. This species differs markedly by the sizes (usually no more than 1,5 meters) and by absence of long rostrum. After detection echolocating abilities of dolphins the first measurements of acoustic activity of harbor porpoise have been made [1,2]. Authors observed acoustic signals with frequencies in a range 2-3 kHz. It is natural, that locating signals with so small frequency actually could not be used for detection of small objects, for example, fishes. The question remained opened before the works executed in Soviet Union under leadership of N.A.Dubrovsky [3]. These data in the subsequent have been confirmed by Danish researcher Mole [4]. Let's notice, that Russian publication has issued practically three years earlier, but in Danish article there are no references to Dubrovsky, Krasnov and Titov's work. In any case, these works have incontestably proved, that low-frequency components are only harbingers of powerful and very high-frequency impulses of this kind of dolphins. Moreover, by present time it is clear, that unlike the overwhelming majority of other dolphins [1,2] harbor porpoise is capable to emit not usual broadband clicks but high-frequency tone bursts including not less of 10 periods of almost monofrequency sound at frequency between 130 and 140 kHz [5-7]. Really, according to the latest data received at a good methodical level in the open sea, the locating signal of this animal, gradually fading, lasts more than 100 mks and includes 15-20 periods [6, fig.5]. The spectral analysis specifies width of this burst at 10-15 kHz. For such signals, however, the consideration exclusively a spectrum hardly is an optimum method of the analysis. Apparently, it is more important to specify, that the time intervals between maxima of the periods are retained with very high accuracy (possibly, shares of micro second). The intensity of a signal reaches 160-200 dB above 1 mkPa even on distance of several meters from an animal [6-7], and in the open sea it essentially above, than in pool [6].

Let's pass now to the description of the basic characteristics of hearing of these animals. The harbor porpoise audiogram have been registered by many methods. They included behavioural experiments [8-10], and various objective methods, including registration of the local evoked potentials of the separate loci located in the brainstem [11,12], skin recorded brainstem activity [13-16], galvanic reflexes [17,18] and evoked potentials of an auditory cortex [19,20]. Practically all these data, excepting early behavioural work [8], incontestably testified to unusually high-frequency hearing of this animal. In some works [9,10] the broad-band sensitivity has been emphasized. These authors also noticed the area of the lowered sensitivity a range 50-70 kHz, where power of clicks of an ordinary

dolphin and bottlenose dolphins is concentrated. Having noted, that this feature can be considered as the adaptation serving for tuning out from possible inferences, we shall concentrate on consideration of hearing in the frequency area exceeding 100 kHz. The registration of local auditory brainstem potentials [11,12] and cortex potentials [20] specify the existence of distinct area of the maximal sensitivity a range 130-140 kHz, that is directly on frequency range of a radiated signal. The same result has been received in detailed research of the acoustical responses registered by a nontraumatic method from of a surface of a head of a dolphin [13-16]. According to some results at downturn of frequency from this optimum thresholds raise on 20-25 dB, and then again decrease [7,8]. According to other data the change of frequency in this direction leads to monotonous raising of thresholds [15,16]. At increase of frequency of a signal from a maximum of sensitivity thresholds rise with a steepness approximately 150 dB per octave.

In many respects the audiogram of this animal reminds audiogram of a bigger horseshoe bat (*Rhinolophus ferrumequinum*) at which the similar area of the maximal sensitivity lays in area 80 kHz [21]. Notice, that this frequency is essentially lower, than at harbor porpoise. As a result, according to the data received by absolutely different methods: behavioural, electrophysiological with registration of potentials of a trunk of a brain, electrophysiological with registration of local cortical responses and, at last, by registration of the unconditional galvanic response we come to conclusion that acoustical sensitivity of this animal reaches up to values nearby 200 kHz. We do not know animals which would possess so high sensitivity at such high frequencies. Possibly, in a range above 150 kHz the harbor porpoise remains to be one of the few, if not the unique animals, capable to perceive and use for the communications some acoustic signals.

Passing to the examination of auditory system features in a range of optimum sensitivity (130-140 kHz), we shall allocate some prominent peculiarities of the analysis of the sounds, observable in this area. First of all, it is necessary to note, that in a corresponding range of frequencies the whole response to tone bursts practically in all cases includes some potentials evoked by a termination of the burst alongside with usual onset potential [12,14,15]. In some cases these reactions are rather close in their sensitivity and amplitude. This unusual property is very typical as well for the bats emitting an initial unifrequency part of a locating signal. Now it is incontestably proved, that these specified animals (the most investigated ones are big horseshoe bat and a moustached bat - *Pteronotus parnellii*) use comparison of frequency of a monofrequency site with echo signal frequency (Doppler frequency shift) for determination the speed of the rapprochement to the target. [22-26]. Experimental data show, that these off-responses arises already on periphery of the bat auditory system owing to an original structure of basilar membranes in these animal. This peculiarity provides extremely high frequency selectivity in rather narrow band of frequencies [22-24]. According to our electrophysiological works in the harbor porpoise responses to the terminations of a signal are also more typical for peripheral part of the auditory pathway. In this connection, a special interest gets the fact, noted by American scientist Darleen Ketten – a specialist in the morphology of auditory periphery of cetacean. She has paid attention, that the structure of a cochlea in harbor porpoise reminds a cochlear structure in a moustached bat [27].

All considered data allow us to put forward the assumption that the harbor porpoise can estimate speed of the rapprochement with a target, using perceived Doppler frequency changes between emitted tone burst and echo signals. Let's try to receive a rough estimations of such opportunity. At speed of 36 km/hours on frequency 130 kHz the value of Doppler frequency shift should make nearby 1 kHz. Meanwhile, the direct estimation of frequency selectivity of this dolphin in this frequency range give the value of differential threshold around 100 Hz [18]. We can come to the same conclusion using information about frequency selectivity of brainstem potentials estimated according to the curves of masking tone by tone in this frequency range [16,17]. It allows to consider that the detection and even the determination of the Doppler shift are quite executable problem for an auditory analyzer of this animal. We shall note also, that during recording of single unit's activity in the inferior colliculus of the bat the differential threshold for frequency classification was estimated as 0,025 % of a carrier [28]. We can see all reasons to consider that the acuteness of the frequency differentiation in neural units of the auditory system of harbor dolphin will appear not worse than the figures which have

experimentally been received at bats. Moreover, it can be even higher, owing to extremely high number of fibres in the acoustical nerve.

Besides, even on such high frequency it is difficult to exclude mechanisms of the time analysis for exploration of the echo signal. The unique ability of dolphins to the analysis of super fine time structure of a signal has been revealed first of all owing to a series of works made by N.A. Dubrovsky with colleagues during the seventieth years of the last century. In particular they discovered, that as the basic attribute of distinction of artificial spherical targets some dolphins (in the given experiments the bottlenose dolphin had been investigated) uses the value of a time interval between primary echo and a signal reflected from a back wall of a target [29,30]. The values of these intervals was in the range tens micro seconds. It meant, that the dolphin can catch the distinctions making units of micro seconds. Experiments using computer model of auditory periphery have precisely shown that such unical sensitivity is really possible. The main preconditions of such sensitivity should be a big number of parallel channels and the presence of uncorrelated high-frequency noise in each of these separate channels [31]. The big number of channels (auditory nerve fibers) really corresponds to features of auditory periphery of investigated object [32]. The assumption of presence of the high-frequency noise leading to powerful spontaneous activity of auditory nerve fibers also is quite lawful so as these features are present at an acoustical nerve of all investigated mammals.

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**D.N.Lapshin**

### ECHOLOCATIONAL SYSTEM OF NOCTURNAL LEPIDOPTERA

Institute for information transmission problems of the Russian Academy of Sciences  
(Kharkevich Institute)  
Bolshoy Karetny per. 19, Moscow, 127994, Russia  
Tel.: (495) 952-33-03; Fax: (495) 650-05-79  
E-mail: lapshin@iitp.ru

*Noctuid moths (Lepidoptera, Noctuidae) are the only group of arthropods that was experimentally shown to possess impulse echolocation. They produce short ultrasonic clicks of 25-190 μs in duration with main spectral peaks from 20 to 140 kHz. The echolocational system is working in coordination with vision and is primarily intended to estimate the position of surrounding obstacles in the near field, i.e. 6-17 cm around the moth. Within that range the moth's ultrasonic locator has a high sensitivity margin. The latency of motor response after the perception of an echo is equal to the wingbeat duration (25 ms). Such a high performance is achieved by direct synaptic contacts between the auditory and the motor neurons within the central nervous system. The discovery of echolocation in invertebrates allows to consider it as a general phenomenon. This hints to a common principle of development of echolocation in various animal groups.*