Echo-Processing Procedure in Bottlenose Dolphins

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Abstract – **For investigation of the echo-processing mechanisms in dolphins a set of logically interrelated tests is developed. In these experiments animals are trained to differentiate simulated echo-like signals and echoes from actual targets. Application of this set of tests to the Black Sea bottlenose dolphins revealed that signal components highlighted within a time interval ~0.2 ms are shown to produce a merged auditory image in dolphins' perception. By analysis of echo within this time window, dolphins utilize three independent discriminative features being determined by the different scale of spectral density oscillations of the echo and by its energy. The animals do not assess differences in signals' polarity. The invariant hierarchical relations between these features were found out, and the structure of the hierarchy was established. The ability of animals to evaluate an average value of the dominant feature in a series of echoes was demonstrated as well. The decision rule describing the process of echoes identification by the dolphins is stated.**

I. INTRODUCTION

The sonar system of dolphins makes available to detect and recognize small size underwater targets with effectiveness unattainable by existing technical devices. Animals, interrogating their environment, use echolocation pulses, which, having been registered chaotically, are rather different in structure and duration. Herewith, frontally transmitted pulses, which provide dolphins maximally informative echoes, are almost standard, one and a half period clicks approximately 8-12 μs in duration, with peak frequency of about 80 -120 kHz [1-2]. Typical echoes produced by such clicks are multiple highlights with a complex structure dependent on the physical characteristics of target and its orientation.

In our tests we investigated mechanisms of echo processing in dolphins, – the mechanisms, that provide extraction of the distinct features from the echo and creation of its subjective image. Accordingly, our attention was focused on the echo-processing procedures taking place within the 'critical interval of time' (CIT) in dolphin sonar. The CIT, – one of the most important parameters in dolphins, – determines the size of time window, within which echo is transformed into a merged auditory image. Despite of existing diversity in assessments of this sonar characteristic [3-6], planning our tests we proceeded from the opinion, that CIT is equal approximately to 0.2-0.3 ms. (Ought to be noted that the data we obtained had confirmed the validity of this prerequisite). In our experiments bottlenose dolphins were trained to differentiate two types of stimuli: artificial echo-like signals with especially combined components, and echoes from various targets, recorded beforehand separately off animals. The advantage of artificial stimuli consists in opportunity to make precise monitoring of the dolphins' reactions to one or other physical components combined in these stimuli. It was reached due to the possibility of creation of any composition of components with any combinations of values of these components in simulated signals. – It is practically unattainable task in a case of echo-signals from actual targets. We could disregard, however, some of the specific echo-processing mechanisms, using in experiments echo-like impulses only. The tests with actual echoes were filling somehow this gap.

In detail the experiments we conducted had been represented for the first time in Ph.D. dissertation [7] and partly in the later articles [8-10]. These tests are the logically interconnected whole. For this reason we have decided to represent here all data at once, inevitably causing some damage to the paper. In particular, some of the experiments will be described briefly, without the appropriate figures and tables.

II. EXPERIMENTS WITH SIMULATED ECHO-LIKE STIMULI

A. Methods

In the experiments of this section (sixteen ones in total) we searched the role of various physical components in the process of signal's image formation in dolphin perception. Echo-like stimuli were produced by shock excitation of spherical (10-mm in diameter) piezoceramic transducer by different single and paired electrical video-pulses (rectangular pulses). Thus, the acoustic stimuli represented a response of the transducer to the jumps of potential in these pulses. The time profile of a single clicks or the large-scale structure of signals' power spectrum density (PSD) was varied by changing duration of single video-pulses (within the interval 6 - 26 μs). We varied the small-scale periodic oscillation of stimuli PSD by changing duration of interpulse interval in paired video-pulses (up to 0.5 ms). In addition, we were able to vary power of stimuli and their polarity independently by changing amplitudes of video-pulses and reversing their polarity.

Each experiment, represented in this section, consisted of two parts. During the first one the dolphin was trained to differentiate signals of two types

presented to animal serially, from the single transducer. Repetition rate of signals in series was equal to 20 ones per second. Signals were presented in random order, with equal probability of signal type occurring. When one of them (the 'positive' signal) was presented, the dolphin was required moving from the start position toward the transducer. The animal got a fish for the correct response. Upon presentation the second, i.e. the 'negative' signal, the dolphin was required remaining at the start position. Once the dolphin had achieved stable differentiation, test signals were presented under the same conditions, along with 'positive' and 'negative' ones (the second part of experiment). Herewith, only the dolphin's 'swim' responses to the 'positive' signals were accompanied by food reward. The functional significance of the components being analyzed in each of these experiments was manifested in the dolphin's responses to the test signals, having been occurring after the previous differentiation tasks.

We have also conducted two control tests, in which we established that dolphins utilize the 'positive' signal (rewarded by a fish) as the reference, i.e. demonstrate 'swim' responses only to the signals conterminous with the 'positive' one in their perception, and ignore any other stimuli.

B. Revealing of the Discriminative Features

We describe in detail the ***experiment # 1*** in order to demonstrate this set of tests. The different scale variations of the signal's PSD were analyzed in this one (Table 1, Fig. 1). The 'positive' (1) and the 'negative' (2) paired signals differed both in large-scale structures of the PSD (envelopes of PSD) and in their small-scale structures (periods of oscillation of PSD). Two test signals (3, 4) of this experiment contained crossed combinations of the values of analyzed components. The first test signal (3) had the envelope of PSD of the 'positive' stimulus, and period of oscillation of PSD the same, as in the 'negative' one. Conversely, the second test signal (4) coincided with the 'negative' in the envelope of PSD, and had the period of oscillation of PSD identical to that of the 'positive' stimulus.

The differences in values of the original signal pair (1, 2) exceeded considerably appropriate differential thresholds in dolphins. For that reason the animal had made correct decisions quite easily during the first part of the test. At the beginning of the second part of the experiment the first test signal had been identified by the dolphin with the 'positive' one, up to ~240th presentation, but the second test signal was ignored (Fig. 2). Toward the end of the test 'swim' responses of the dolphin to the first test signal disappeared due to no rewarding. Thus, we can conclude that the dolphin, discriminating the initial pair of signals, preferred the envelope of PSD as the distinctive feature. The animal did not pay attention to differences in the period of oscillation of PSD between the 'positive' and the first test signals, having identified them at the start of the second part of test. The dolphin had included another component in account later, when it had become necessary for solving the task in changed conditions.

Obtained results enabled us to conclude that both components, analyzed in this experiment, are perceived by the dolphin as independent features, and the envelope or macrostructure of PSD (feature MaPS) is dominant in animal perception over its small-scale oscillations or microstructure of the PSD (feature MiPS).

TABLE 1
PARAMETERS OF ELECTRICAL VIDEO-PULSES APPLIED IN EXPERIMENT # 1. WE HIGHLIGHTED BOLD IN TABLE THE VALUES OF ANALYZED COMPONENTS IN 'POSITIVE' SIGNAL AND THOSE OF THEM IN TEST STIMULI, WHICH ARE THE SAME AS IN THE 'POSITIVE'

The type of stimulus	First pulse duration (μs)	Sec. pulse duration (μs)	Interpulse interval (μs)	Amplitude (V)
'Positive' signal	**15**	**15**	**100**	50
'Negative' signal	20	20	150	50
First test signal	**15**	**15**	150	50
Sec. test signal	20	20	**100**	50

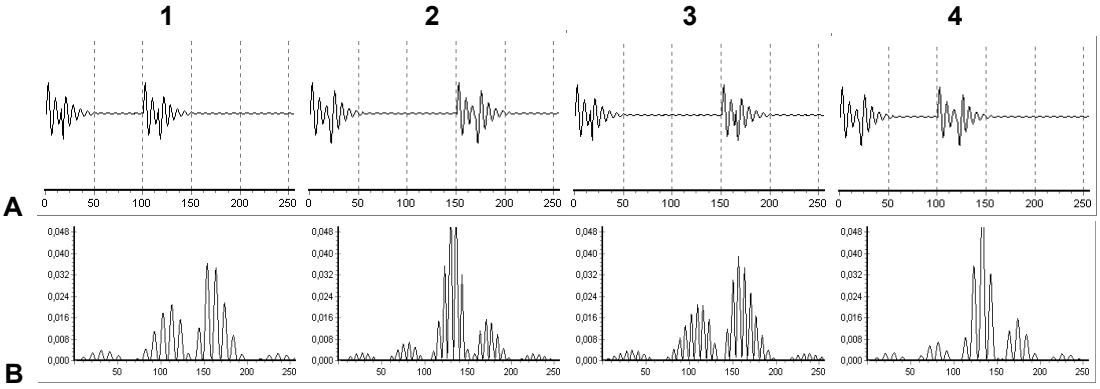

Fig. 1. Time profiles (A) and PSD (B) of the 'positive' (1), 'negative' (2), first test (3), and second test (4) stimuli exposed in the experiment # 1.

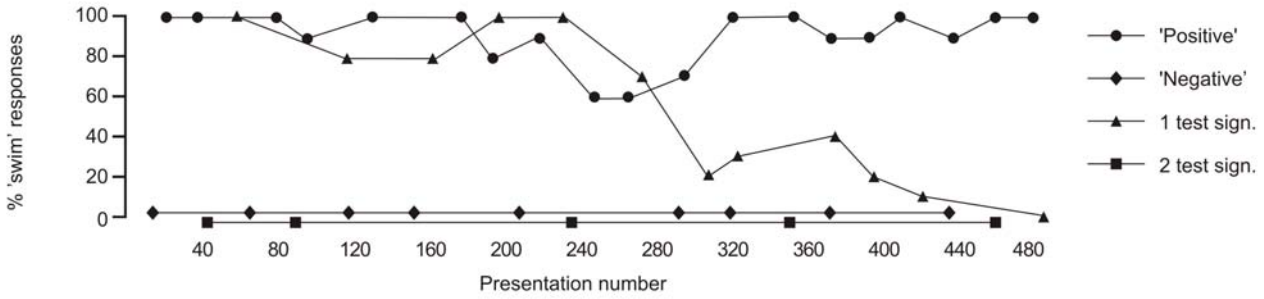

Fig. 2. Dynamics of variation of the dolphin's responses to signals presenting in the experiment # 1 (second part). Each calculated point of the graph represents the percentage 'swim' responses to a set of ten consecutive presentations of the appropriate stimulus.

By this way exactly, we had received the following results, presenting to dolphins various physical components of signals, combined in pairs:

Dolphins cannot distinguish signals differing only in their polarities. Animals perceive PSD of the single impulse and its amplitude independently, and feature related to PSD is dominant over the amplitude. – Dolphins prefer feature related to PSD in distinguishing of single pulses, and include amplitude in analysis, when it becomes impossible to use only the differences in PSD for solving a task. Minority of the energy in relation to feature MaPS, as well as to feature MiPS, was demonstrated in paired signals as well. Dolphins check features' values successively, passing from the dominant feature to the minor one. Animals interrupt this process, just having reached the feature containing detectable differences in compared signals.

D. Robustness of Features' Hierarchy

The dominance of one feature over the other in analyzed pairs of components was determined by dolphins' free selection of a given feature as a distinctive one during the first parts of above experiments. This hierarchy, however, could be caused by unsuccessfully chosen differences in the values of the compared components. It was not clear, whether the established hierarchical structure would be preserved for any other relations between the differences in the values of these components.

The robustness of the above revealed hierarchy was checked by the following way. The 'positive' and the 'negative' signals in each experiment of this series differed only in the values of feature revealed previously as minor one in pair. In this way the dolphin was intentionally compelled to accept this feature as the distinctive one during the first part of the experiment. The value of this feature (distinctive, in a given case) in the test stimulus (the second part of the experiment) was the same as in the 'positive' signal, but the value of feature determined previously as the dominant one in pair was altered. Identification by an animal of the test stimulus with the 'positive' signal would indicate the relative nature of the previously established hierarchy, and its decision to ignore this stimulus would confirm strong robustness of this hierarchy.

We represent this series on an example of the ***experiment # 2*** (Table 2). Original pair of signals differed in the values of energy only. The value of feature MaPS was altered in the first test signal, as well as the value of feature MiPS in the second test stimulus (highlighted bold in table).

The result of this experiment (Fig. 3), as well as of others in this series, showed that the dolphins ignored confidently the test stimuli. This fact demonstrates the invariance of the established hierarchy under the disproportional conditions of the tests.

E. The Structure of Dolphin's Feature Space

Two strings of features were established in previous tests in single and paired stimuli: 1) signal's PSD and its energy for single pulses, and 2) features MaPS, MiPS, and energy for paired ones. On the other hand, established procedure of the 'step-by-step' analysis of the features by dolphins from senior to minor seemed to contradict somehow to the presence of two feature strings simultaneously. One hierarchical sequence of features would seem to be more adequate for such procedure. We could eliminate this ambiguity, conducting the ***experiment # 3***. The first and the second test signals of this experiment represented the single copies of the paired 'positive' and 'negative' stimuli, accordingly (Table 3, Fig. 4). Therefore the PSD

TABLE 2
PARAMETERS OF ELECTRICAL VIDEO-PULSES APPLIED IN EXPERIMENT # 2. WE HIGHLIGHTED BOLD IN TABLE THE VALUES OF COMPONENTS DEFINING HIGHER FEATURES (MIPS AND MAPS), WHICH WERE ALTERED IN TEST SIGNALS

The type of stimulus	First pulse duration (μs)	Sec. pulse duration (μs)	Interpulse interval (μs)	Amplitude (V)
'Positive' signal	13	13	160	50
'Negative' signal	13	13	160	25
First test signal	**16**	**16**	160	50
Sec. test signal	13	13	**100**	50

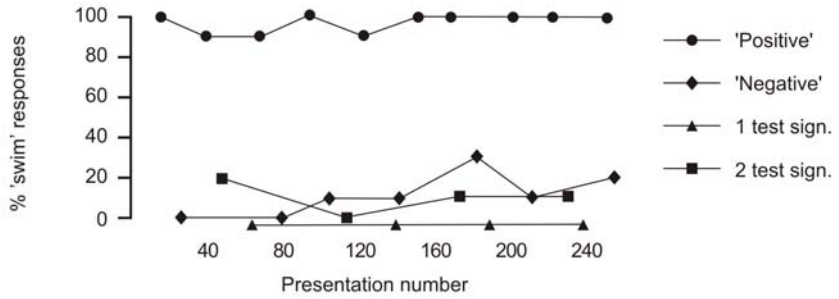

Fig. 3. Dolphin's reactions to the test signals exposed in the second part of experiment # 2. Each calculated point of the graph represents the percentage 'swim' responses to a set of ten consecutive presentations of the appropriate stimulus.

TABLE 3
PARAMETERS OF ELECTRICAL VIDEO-PULSES APPLIED IN THE EXPERIMENT # 3. WE HIGHLIGHTED BOLD IN TABLE THE COMPONENTS DEFINING FEATURE MAPS IN THE 'POSITIVE' SIGNAL AND FIRST TEST ONE

The type of stimulus (Paired signals)	First pulse duration (μs)	Second pulse duration (μs)	Interpulse interval (μs)	Amplitude (V)
'Positive' signal	**15**	**15**	100	50
'Negative' signal	20	20	100	50
(Single signals)	Pulse duration (μs)		Amplitude (V)	
First test signal	**15**		50	
Second test signal	20		50	

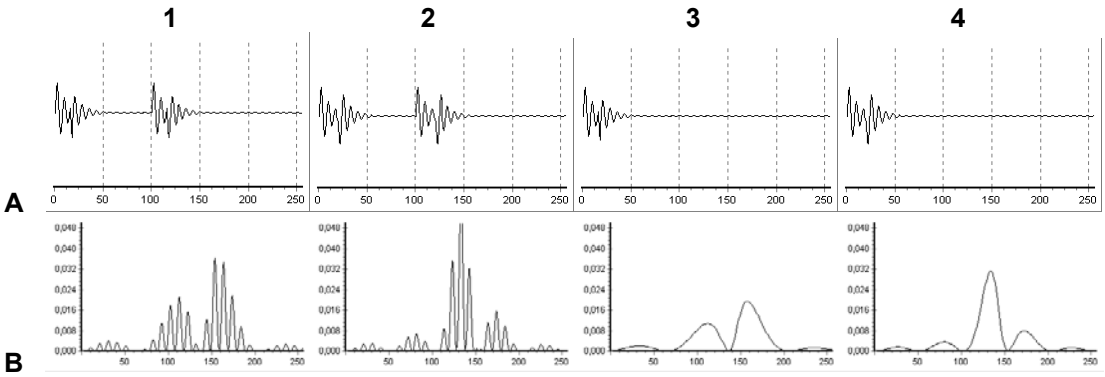

Fig. 4. Time profiles (A) and PSD (B) of the 'positive' (1), 'negative' (2), first test (3), and second test (4) stimuli exposed in the experiment # 3.

of these signals coincided qualitatively with the envelopes of PSD of the 'positive' and the 'negative' ones. At the beginning of the second part of this experiment (Fig. 5) the dolphin identified the first test signal and the 'positive' one. Toward the end of the test this behavioral reaction disappeared due to lack of rewarding. Thus, the animal had identified at the first step paired signal and a single one having both the same large-scale structure of the PSD, i.e. verified the feature MaPS only. Destruction of the image of the

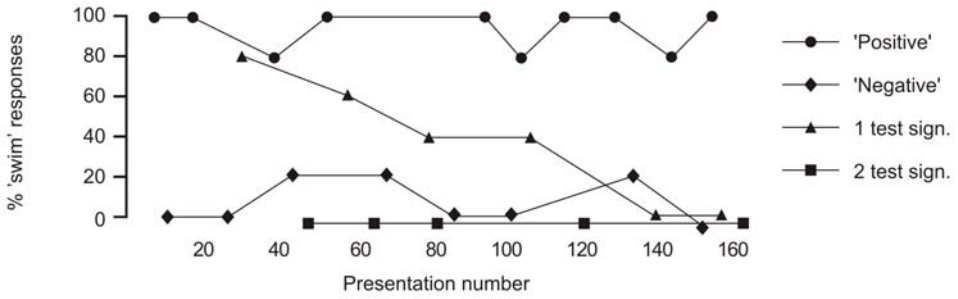

Fig. 5. Dolphin's responses to the signals presented in the experiment # 3 (second part). Each calculated point of the graph represents the percentage 'swim' responses to a set of five consecutive presentations of the appropriate stimulus.

'positive' signal in the first test one in animal's perception occurred at the second step, when the dolphin included the feature MiPS in analysis. This result eliminates the above mentioned contradiction. The signal-processing mechanism of dolphins contains one string of features ranged as follows in order of significance: MaPS, MiPS and Energy.

F. The Boundaries of the Domains of Definitions of Features MaPS and MiPS

It was shown at a qualitative level that different scale variations of the signal's PSD govern the features MaPS and MiPS. The boundaries of the domains of definitions of these features were assessed quantitatively in the ***experiment # 4***. At the first part of this test the dolphin differentiated two paired signals with intervals of 120 μs between the pulses. All four pulses constituting the pairs in the 'positive' and 'negative' signals had different time profiles. Paired signals, used as the test stimuli at the second part of the experiment, had the same pulses structures as in the 'positive' one, but randomly varied interpulse intervals in the range 50-500 μs. Herewith, the dolphin's 'swim' response to any of the test stimuli was reinforced with a fish ('non directed reinforcement') in order to prevent the animal from initiating analysis of the MiPS feature and also to ensure an equivalence of conditions for all test stimuli.

We knew beforehand (the above reported data) that the dolphin would utilize only the dominant feature MaPS during the first part of the experiment. Thus, it was known in advance that the animal would identify as 'positive' any signal conterminous with the 'positive' stimulus in the value of this dominant feature. The test signals were composed of pulses having the same time profiles as the pulses of the 'positive' stimulus. Consequently, the value of feature MaPS should be the same in both cases within certain limits of variation of the interpulse interval. This value should be lost, on the one hand, when the pulses of the test signal would be separated by time intervals greater then the CIT. – Since the merged auditory image of the pair of pulses with different time profiles within the CIT does not coincide with the separate auditory images of these pulses outside this interval. This interpretation should specify an upper boundary of the domain of definition of feature MiPS (in temporal expression), or the value of CIT at the same time. On the other hand, successive narrowing of the interval between the pulses (δT) in the test signals and one-to-one related increase in the oscillation period of PSD (δF), – as $\delta F=1/\delta T$, – should inevitably distort the envelope of PSD of the pair, i.e., disrupt the value of feature MaPS. This, in turn, may show a definite boundary between the investigated features.

The subsequent results confirm the validity of the above stated hypothesis (Fig. 5). The reversals of the dolphin's 'swim' responses to test stimuli, caused by above-mentioned consideration, took place at interpulse intervals ~100 μs and ~200 μs (at a 75% 'swim' response), which correspond to the periods of oscillation of PSD ~10 kHz and ~5 kHz, in the spectral expression.

We have received ~75 μs (~13 kHz, in spectral expression) instead of above 100 μs in analogous experiments, applying shorter pulses to the 'positive' signals. – The envelope of PSD of these signals has appeared steadier against destruction. Conditionally, we will use further the value of ~80 μs (~12 kHz, in spectral expression) to designate the boundary between features MaPS and MiPS.

G. Discussions

Summarizing results obtained in this section, we can conclude that for distinction of signals within CIT bottlenose dolphins utilize three independent, hierarchically interrelated discriminative features with the following diminishing significance: 1) Feature MaPS, being defined by large-scale variations of signal's PSD, exciding ~12 kHz frequency bandwidth; 2) Feature MiPS being defined by small-scale oscillation of signal's PSD with the periods in the interval ~5-12 kHz; and at last, 3) Feature Energy, being defined by the energy of signal within CIT.

The bottlenose dolphin, distinguishing signals, estimates successively features' values from senior to minor, terminating the process at the feature, which contains detectable differences in compared stimuli (the distinctive feature). Subsequent identification of the reference signal obeys the following decision rule: If the dolphin utilize a particular feature as the distinctive one, then in order to preserve the image of the reference signal, it is necessary and sufficient to preserve the same values of the distinctive feature and all higher ones in order of hierarchy.

Let's note also that an estimation of the dominant feature (MaPS) by bottlenose dolphins seems to be an obligatory link in signals processing. – Two other features (MiPS and Energy) may remain outside of animal's attention, when it is possible to make decision by the values of the MaPS feature. This fact explains a controversy of the experiments, in which an ability of bottlenose dolphins to discriminate time intervals (over a wide range of change) was measured [11]. The dolphins (six animals in total) have failed to distinguish interpulse intervals exceeding considerably the appropriate differential thresholds. In these experiments the pairs of noise bursts, and high-frequency pure tone bursts with random phases and 50 μs in duration were used. It made difficult or even impossible an estimation of MaPS feature. For this reason the dolphins did not proceed to the analysis of the following feature in hierarchy (MiPS), quantitatively accessible to distinction by animals, and thereby could not solve such easy (from the first consideration) task.

In accordance with the results, reported above,

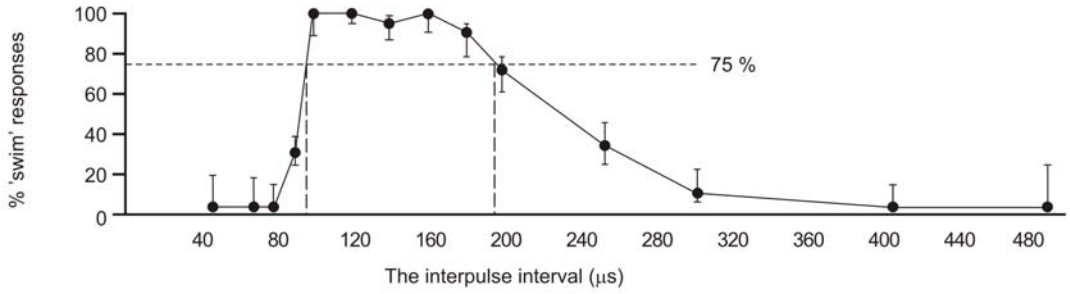

Fig. 6. Percentage 'swim' responses of the dolphin to test signals exposed in the second part of the experiment #4. The vertical segments indicate the confidence intervals at the 5% significance level.

multiple highlights limited by the CIT produce a merged auditory image ('shot') in dolphin's perception. It, likely, should mean existence of a zone of reduced auditory attention (sensitivity) of animal in immediate proximity after the CIT. However, the paper [12], published recently, demonstrates high sensitivity of the bottlenose dolphin to slight differences in the center frequencies of low-amplitude highlights, trailing after high-amplitude one, directly after the CIT. We should recognize that these results, in aggregate with our data, obviously raise new questions in this area of researches.

III. EXPERIMENTS WITH ACTUAL ECHO-SIGNALS

Echo-signals were recorded at a sea coastal zone, at high intensity ambient noise, at a distance 10-15 m from targets. Targets were insonified by short clicks simulating the bottlenose dolphins' echolocation signals, with peak frequency at 50 and 120 kHz and repetition rate 20-80 pulses per second. Dolphins distinguished echoes from two various targets in each test. Animals were required to distinguish echoes from the same target recorded at different weather conditions (calm and waves) in the last experiment only. The stimuli were presenting to a dolphin by series, from the same transducer, randomly, with equal probability of occurring. The series' duration did not exceed 5-7 s.

Animals distinguished easily all types of stimuli in our experiments (with 90–100% of correct responses) except the last pair only (about 50% of correct responses). At the same time, the study of echo-signals showed us significant fluctuation of their PSD, which excluded absolutely an opportunity to form steady MaPS feature values by analyzing echo-signals separately. We saw in experiments with echo-like stimuli that a dolphin, processing signals, makes an estimation of their MaPS values in all cases, independently of an informative expediency. The fact of successful distinction of the real echoes by dolphins, hence, should be considered as the fact of estimating by animals the feature MaPS values in these echoes. The above-stated reasons, in aggregate, resulted us in an idea on utilizing by dolphins of MaPS values by averaging over series of echoes. We have found out confirmation to this, having distinguished echoes in computer by comparison of averaged values of their PSD envelops. At the same time we did not manage to distinguish by this way the pair, inaccessible to distinction by dolphins.

This result is coordinated well with the data represented in [13]. It was shown that a dolphin is able to estimate average values of interpulse intervals varying randomly within the limits of 50-200 μs. It coincides practically with the range of definition of the feature MiPS established above. This ability of bottlenose dolphins to evaluate average values of the first two features in hierarchy, MaPS and MiPS, entitles the assumption on probable ability of animals to evaluate also an average value of the feature Energy.

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