PHYSIOLOGICAL INVESTIGATION OF THE DOLPHIN BRAIN

22 MAY 1979 (FOUO 16/79) 1 OF 2

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TRANSLATIONS ON USSR SCIENCE AND TECHNOLOGY
BIOMEDICAL AND BEHAVIORAL SCIENCES
(FOUO 16/79)
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Moscow ELEKTROFIZIOLOGICHESKOYE ISSLEDOVANIYE MOZGA DEL'FINOV in Russian 1978 signed to press 27 Jun 78 pp 2-6, 86-160, 201-208, 211-213

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[Annotation, introduction, table of contents, Chapter 3 and bibliography from book by A. Ya. Supin, L. M. Mukhametov, et al., Izdatel'stvo Nauka, 1200 copies, 215 pages]

Annotation

[Text] This book summarizes experimental data in an area not previously investigated--the physiology of the brain of Cetaceans--which are of interest for both comparative physiology of the nervous system and general neurophysiology. These data include information on the unusual nature of the arrangement of the sensory areas of the cerebral cortex in dolphins and the unusual nature of the generation of electrical reactions (evoked potentials) in the cortex; the unique nature of the regulation of wakefulness and sleep (the alternating development of sleep in the two cerebral hemispheres); features of the auditory system that can be revealed according to the electrical reactions of the cerebral cortex. Methods of electrophysiological investigation of the dolphin brain are discussed.

The book is intended for biologists specializing in neuromorphology and neurophysiology, zoology and ecology.

It has 102 illustrations and a bibliography of 160 titles.

INTRODUCTION

The interest which dolphins have aroused among researchers working in the most varied areas of science is caused by many factors and is, to a considerable extent, to be expected. Hardly any other animal which has become available for research has immediately posed such a number of diverse problems for specialists in various fields. The characteristics of these animals' behavior, which is organized in an extremely complex manner; their striking ability to learn quickly and to enter into contact with man; their developed system of communication by sound; their highly-developed hearing, including the ability to perceive ultrasonic signals; their capacity for active echolocation; their brain, which is enormous (for animals); their ability to move about in water at high speeds with a relatively small energy expenditure and their capacity for prolonged diving--all of this is far from being a complete list of the anatomical and physiological characteristics of dolphins, which deserve the most careful study.

Do dolphins (or Cetaceans in general) actually constitute a group of animals that are exceptional in their morphophysiological characteristics and deserve very special attention from researchers? Hardly. Rather, dolphins provide an instructive example of how expanding the range of animals which are the objects of detailed morphophysiological study can be unexpectedly important and useful.

Unfortunately, a significant gap exists between the tremendous number of animal species which are within the sphere of attention of zoologists with a broad range of specialties and the number of species which have become model objects for detailed study of their morphological or physiological organization. This limitation of the number of objects for detailed study is, in fact, essential. The constant intensification of the research requires a thorough knowledge of the object, which would scarcely be possible with a large number of objects. On the other hand, for a comparison of the various works, it is advisable for studies to be performed of the same standard objects. Consequently, the selection of a relatively small number of animal species as standard laboratory subjects is dictated by the logic of biological research.

This situation also has a reverse side, however: one cannot always be confident that the data discovered in the course of the investigations reflect universal phenomena and do not merely describe the features of the species being studied or of the group to which this species belongs. For this reason, detailed morphophysiological study of new species may sometimes lead to unexpected results.

This is precisely what happened when dolphins in captivity became available for detailed study as a result of the opening of oceanaria-dolphinaria in a number of countries. In this case, the morphologists and physiologists did not acquire simply one more object for study, but an animal differing radically from the well-known laboratory mammals. In the course of their evolution, the Cetaceans quite early separated from the main trunk of the evolutionary tree of the mammals and followed an extended developmental path, independent of the land mammals. For this reason it is quite natural that many of the problems of environmental adaptation were solved in a unique way in this direction of the evolution of mammals and that many features of the Cetaceans' morphophysiological organization proved to be unusual for researchers working with land laboratory animals.

An understanding of the fact that the interest in dolphins is due to their difference from the well-studied laboratory animals rather than to any uniqueness of their position in the animal world reveals the fullest significance of the investigations being made of dolphins. They are important primarily because they can rid us of a one-sided concept of a number of aspects of mammalian organization. It should be particularly emphasized that the comprehensive study of an unusual order such as the Cetaceans is definitely of exceptional interest for an understanding of many questions of mammalian evolution, including the evolution of the brain.

One of the most important and interesting questions in the study of Cetaceans concerns the organization of their nervous systems. The Cetacean brain is one of the largest in the animal world. Although it is difficult to compare the dimensions of the brain in animals with differing body size (neither absolute nor relative brain weight, nor the product of absolute weight multiplied by the relative weight is considered to be a universal criterion for such a comparison), the enormous and complex brain of the dolphins, nevertheless, could not fail to draw extremely close attention from neuromorphologists and neurophysiologists.

The study of the brain can be effective, however, only if there is a harmonious combination of morphological and physiological investigations. But while the study of the morphology of the Cetacean brain (which is more accessible) has a relatively short history, until recently there were practically no neurophysiological studies at all.

There are quite definite reasons for the inadequate development of neurophysiological, and particularly electrophysiological investigations of the Cetacean brain. Despite the fact that dolphins have been held in captivity successfully for many years, until recently they remained expensive and unavailable animals, the experimental use of which was extremely limited. Furthermore, many difficulties directly related to experimental methods are encountered in the performance of neurophysiological investigations of dolphins. The characteristics of the dolphins' structure and physiology make it difficult or impossible to apply to them many well-developed methods that are used in working with the usual laboratory animals. In addition to the fact that the methodology for working with dolphins had to be developed anew to a significant extent, there were, at the same time, serious difficulties to be overcome, stemming from the problems of access to the brain of these animals, the need to take special measures to preserve their lives during operations and experiments, etc. At the same time, the methodological problems are intensified by humanitarian requirements: in working with highly organized animals, a category which definitely includes dolphins, it is essential to exercise strict control and to limit the traumatic effect of the research methods that are used, avoiding gross vivisection.

The interest in the neurophysiology of the dolphin brain, however, has forced us to look for ways to overcome these difficulties. Attempts have repeatedly been made to perform physiological investigations of dolphin brains (Langworthy, 1932; Yanagisawa et al., 1966; Lende, Adikman, 1968, and others), although the majority of these attempts have yielded few results or have been unsuccessful due to the above-mentioned methodological difficulties. Until recently the literature contained only isolated reports of successful work on the electrophysiological study of the dolphin brain. Among the pioneers of such investigations, Bullock and his coauthors (Bullock et al., 1968) should particularly be mentioned.

The Laboratory of the Evolution of the Sensory Systems of the Institue of the Evolutionary Morphology and Ecology of Animals of the USSR Academy of Sciences, which is represented by the authorial collective of this book, is one of the few laboratories that conducts electrophysiological investigations of the dolphin brain. Various aspects of the morphological and physiological organization of the brain of the dolphin have been studied by this laboratory for a number of years. Furthermore, studies of a comprehensive and systematic nature are considered to be one of the main goals of this laboratory.

It goes without saying that certain limitations on the work volume were nevertheless inevitable. The cerebral cortex, the highest analyzing center, was chosen for more detailed study, although other brain centers were studied along with it. A number of issues requiring priority investigation were outlined. They included, particularly, the problem of the main features of the general morphophysiological organization of the dolphin brain, and especially of the cerebral cortex. The dolphins' analyzer activity was thought to be the second important problem, with the dolphins' key, acoustic analyzer attracting priority attention. Finally, it appeared that the regulation of sleeping and waking states--in connection with features of the dolphins' biology and behavior--deserved special attention.

In practice, during the process of the investigations all these problems proved to be interrelated to a significant degree, and were worked on as a single unit. The division of all the results obtained in these areas, however, proved to be convenient for purposes of their systematization, and formed the basis for the contents of this book.

The major part of the investigations, the results of which form the basis of this collective monograph, was carried out during expeditions to the Black Sea, in the area of Anapa and Novorossiysk, rather than at stationary bases or in oceanaria. The authors note with gratitude that it would have been impossible to carry out the research program of the expeditions without the help of a large number of assistants who participated in the labor-consuming auxiliary work. The authors would like to express sincere gratitude to everyone who assisted with the investigations. The authors will also be grateful to their colleagues for any critical comments.

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CHAPTER 3. DETERMINING THE CHARACTERISTICS OF HEARING IN DOLPHINS FROM THE ELECTRICAL REACTIONS OF THE CEREBRAL CORTEX

By recording the electrical reactions of the cerebral cortex to various afferent stimuli, important information may be obtained on the mechanisms of analysis of these stimuli and on the properties of the corresponding analyzer. If one takes into consideration the exceptional development of dolphins' acoustic analyzer, as well as the fact that they have the capacity for acoustic location, it is clear that the acoustic analyzer attracts the greatest attention when studies of this type are made of the dolphin's brain.

The characteristics of hearing in dolphins have drawn the attention of a number of researchers. After it was discovered that dolphins can perceive ultrasonic frequencies (Kellog, Kohler, 1952; Schevill, Lawrence, 1953), attempts were made to measure more precisely the characteristics of the dolphins' auditory system, particularly its absolute sensitivity and frequency-threshold characteristics.

The first sufficiently detailed quantitative studies of hearing in dolphins were made on specially trained animals under free behavioral conditions. The animal was taught to perform a certain movement in response to a sound signal. By gradually reducing the intensity of the signal, it was possible to establish the minimum intensity at which the signal could still be perceived by the animal, which was indicated by the performance of the control movement. This value was taken as the threshold of perception of the signal. By using pure tones of varying frequencies as the signals, it was possible to determine how the sound perception threshold depends on its frequency, i.e., to draw up an audiogram.

Measurements made in this way (Johnson, 1967) showed that the minimum thresholds of auditory perception in dolphins T. truncatus are observed at frequencies of about 50 kHz, where they are (if the original data from the system of units used by the author are converted into the International System) less than 10^{-3} n/m^2, corresponding to a power of about 10^{-13} w/m^2. Quite low thresholds are characteristic of the perception of sounds with frequencies ranging from approximately 20 to 100 kHz, and with a stronger difference in the frequency of the sound from the optimum threshold, they rise:

toward the lower frequencies--more slowly, and toward the higher frequencies --quite sharply, since at a frequency of 150 kHz in the work mentioned the thresholds exceeded the thresholds for the optimum frequencies by approximately 60 db.

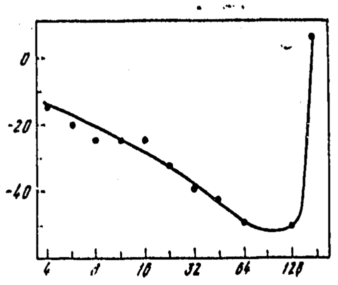
The disadvantage of this methodology, however, is its extreme labor-intensiveness and the very long time taken for the experiments, as well as the need for good training of the animal. This makes it difficult to repeat the experiments and reproduce the data obtained when many animals are used. All Johnson's data were obtained by using the same dolphin. Subsequent analogous studies were also made using a single animal: on a bottlenose dolphin, T. truncatus (Ayrapet'yants et al., 1969; Morozov et al., 1971), on the porpoise Ph. phocoena (Andersen, 1970), the whale Orcinus orca Linnaeus (Hall, Johnson, 1972) and on a fresh-water dolphin (Jacobs, Hall, 1972). At the same time, various work performed using dolphins of a single species yielded noticeably varying results. The limited nature of the experimental material made it impossible to decide whether these differences were caused by individual characteristics of the animals being studied or by other reasons.

More efficient is the methodology in which the thresholds of auditory perception in dolphins were also determined by the conditioned reflex method, not under conditions of free behavior, but rather with the development in the secured animal of a defensive conditioned reflex to a combination of a sound signal and electrodermal reinforcement. The vegetative components of the defensive conditioned reflex evoked were recorded (electrodermal reaction, change in respiration, pulse rate, etc.) and according to their manifestation it was possible to judge whether the sound signal was perceived by the animal (Supin, Sukhoruchenko, 1970, 1974; Sukhoruchenko, 1971). The rapidity of the development of the defensive conditioned reflex makes it possible to obtain representative material, duplicating the measurements when many animals are used.

Measurements made in this way using the porpoises Ph. phocoena yielded results similar to the data obtained using bottlenose dolphins. The minimum thresholds of auditory perception were detected at frequencies of 64-90-128 kHz and were less than 10^{-3} n/m^2 (Fig. 36). The minimum threshold values obtained in individual measurements using both dolphins T. truncatus (Johnson, 1967) and porpoises Ph. phocoena (Supin, Sukhoruchenko, 1974) reached 10^{-4} n/m^2, which corresponds to 10^{-14} w/m^2.

Measurements were also made of other characteristics of dolphins' auditory system, including the differential thresholds with respect to frequency and intensity. The measurements of the differential thresholds for frequency were made under the conditions of a behavioral experiment using trained animals, T. truncatus (Jacobs, 1972; Thompson, Herman, 1975) and also under the conditions of developing a defensive conditioned reflex in porpoises Ph. phocoena (Sukhoruchenko, 1973; Supin, Sukhoruchenko, 1974).

The lowest differential thresholds for frequency, obtained in the latter work, were 0.1-0.2%, although in the entire, quite broad range of frequencies studied (from 4 to 180 kHz) they did not exceed 0.5% (Fig. 37).



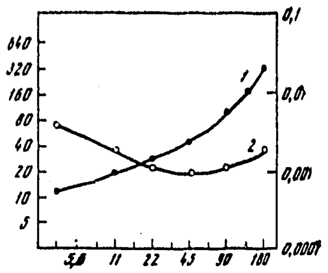


Figure 36. Audiogram of a Porpoise Ph. phocoena, Obtained by the Method of Recording Conditioned Reflex Vegetative Indicators (Supin, Sukhoruchenko, 1974)

Along axis of the abscissa--frequency of the tonal signal, in kHz; along axis of ordinates--threshold intensity of the acoustic stimulus relative to a level of 0.1 n/m^2 db

Figure 37. Differential Thresholds According to Frequency, Measured in the Porpoise Ph. phocoena Using the Method of Recording Conditioned Vegetative Indicators (Supin, Sukhoruchenko, 1974)

Along axis of abscissa--frequency of the tone; 1--threshold deviation (scale on the left, in Hz); 2--relation of the threshold deviation to the initial frequency (scale on the right)

The measurements of the differential thresholds with respect to intensity, made using freely moving dolphins T. truncatus (Burdin et al., 1971b) and porpoises Ph. phocoena (our data) showed that the animals can perceive changes in acoustic pressure of less than 10%. A study was also made of the ability of dolphins' auditory system to differentiate temporal intervals (Thompson, Herman, 1975).

The necessary data on the nature of the functioning of the auditory system of dolphins are not, however, exhausted by information of this type. A study must be made of the mechanisms of operation of the auditory system, particularly the neural mechanisms of analyzing acoustic signals. The main method that may give the necessary information on this problem is the electrophysiological method of study, which makes it possible to record the activity of the sensory neural centers directly during the process of their analyzing afferent signals.

The first attempts at an electrophysiological study of the dolphins' auditory system dealt with the inferior colliculus of the brain (Bullock et al., 1968). The results of this work are particularly discussed in more detail below. There are also attempts to study the electrical activity of other sections of the auditory system, including the inner ear (McCormick, et al., 1970; Ridgway, et al., 1974).

In our experimental research, particular attention was paid to studying the analysis of the acoustic signals in the auditory regions of the dolphins' cerebral cortex. Examined along with this are certain results obtained in an electrophysiological study of other centers of the auditory system--the corpus geniculatum mediale and the inferior colliculus.

1. Microelectrode Investigation of the Pulse Activity of Individual Neurons of the Auditory Cortex

The method of microelectrode recording of the activity of individual neurons should be regarded as a more advanced method of studying information processing in the neural centers at the present time. This method makes it possible to perform a more detailed analysis of the processes taking place in the neurons and affords an opportunity of directly obtaining information that is inaccessible or accessible with difficulty when the method of recording the summated electrical reactions is used. Most modern concepts of the mechanisms of sensory analysis could be formulated only in consideration of the information obtained with a study of the activity of individual neurons.

Therefore, attempts were initially made at microelectrode study of the work of individual neurons in the dolphins' cerebral cortex when analyzing acoustic signals (Gapich, Supin, 1974). These studies were performed under conditions of an acute experiment using porpoises Ph. phocoena. In the animals operated on with a local anesthetic, the actuating part of a distant-reading hydraulic micromanipulator was placed on the cranial bone, and by means of it tungsten microelectrodes with the diameter of the tip in the order of 1 micrometer were introduced into the animal's brain. The main difficulty in recording the activity of individual neurons in unanesthetized and nonimmobilized dolphins is that the sharp movements occurring mainly in breathing may lead to damage or loss of the neuron being recorded. With the use of a remote-controlled micromanipulator and with reliable attachment on the skull of its actuating part, however, this difficulty could be overcome and stable extracellular assigning of the pulse activity of the neurons could be obtained.

One of the main requirements imposed on the work of studying the activity of individual neurons is that a sufficiently large sampling of neurons absolutely must be presented, so that further statistical analysis can reveal what forms of reactions of the neurons may be regarded as typical, what variants of the reactions, types of neurons, etc. exist. When the brain of dolphins is studied, this requirement comes into conflict with the difficulty of access to the material. Therefore, the results of the series of experiments in which we studied the activity of individual neurons of the dolphins' auditory cortex may be considered only preliminary, since the limited nature of the experimental material does not permit significant conclusions to be drawn concerning the special features of analysis of acoustic signals in the dolphin's auditory system.

In this series of experiments (Gapich, Supin, 1974), 45 neurons of the auditory region of the cerebral cortex of the porpoise Ph. phocoena were studied with extracellular assigning of their pulse activity. In addition, for comparison, 31 neurons from the section of the cortex located outside the auditory region (anterior to it) were studied. Most of the neurons had a background activity ranging from 1 to 10 pulses/sec. A certain difference was revealed in the medium frequency of the background activity in the neurons of the auditory and nonauditory regions. In the auditory region, the frequency of the background activity of the neurons was most often 1-6 pulses/sec., as is shown on the histogram of distribution of neurons according to the frequencies of the background activity in Figure 38, A (median of the histogram, 4.4 pulses/sec). In the nonauditory region of the cortex, located toward the anterior, there proved to be numerous neurons with a higher-frequency background activity (Fig. 38, B); the mode of the histogram is 6-9 pulses/sec, and of the median--10.9 pulses/sec.

With respect to the nature of the distribution of the pulses in time, the background activity could be irregular or grouped, with a pulse group repetition period of 40-120 msec. The nature of the background pulse activity is shown in the form of histograms of the intervals between the pulses for different neurons. Irregular activity gives a monomodal distribution of intervals between the pulses, the peak of which corresponds to the length of the most frequently encountered intervals (Fig. 39, A). The grouped activity gives a bimodal distribution of the intervals between the pulses (Fig. 39, B). The first peak of the histogram (0-20 msec in Fig. 39, B) corresponds to the length of the intervals within the groups of pulses and the second peak (60-80 msec in Fig. 39, B) corresponds to the most probable length of the intervals between the groups of pulses.

A considerable number of the neurons of the auditory region of the cortex reacted to acoustic stimuli--clicks or turning on tonal signals. Out of 32 neurons of the auditory region, the reactions of which were studied with the effect of clicks, 14 neurons reacted to this stimulus by activation, 3--by inhibition, and in 15 neurons no reliable reaction was detected. Out of 20 neurons of the auditory region in which the reactions to tonal signals were studied, reactions in the form of activation were detected in 7 neurons, in 1--only an inhibiting reaction, and in 12 neurons no reliable reactions could be detected.

In their capacity to react to acoustic signals, the neurons of the auditory region of the cortex differ substantially from the neurons of the adjacent regions, in which such reactions were practically nonexistent. Out of

23 neurons in the nonauditory region of the cortex, the activity of which was studied with the effect of acoustic stimuli, only in 1 neuron was a reaction to an acoustic click revealed.

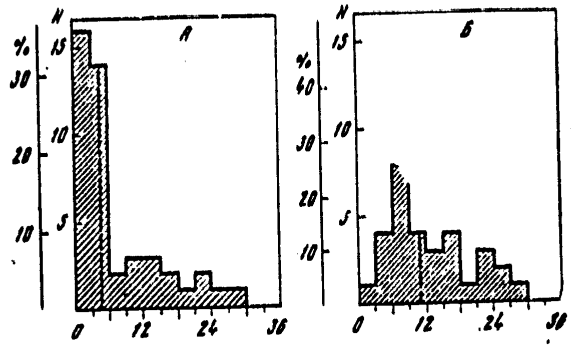


Figure 38. Frequency Distribution of Background Pulse Activity of Neurons in the Cerebral Cortex of the Porpoise Ph. phocoena

A--sampling of neurons from the auditory region of the cortex (suprasylvian gyrus), 45 elements; B--sampling of neurons from the nonauditory region of the cortex, 31 elements. Along the axis of the abscissa--the frequency of the background pulse activity, in pulse/sec; along the axis of ordinates--number of elements in each class of histogram, absolute and in % of total number of elements in sample. Vertical dotted lines--medians of the histograms

In the auditory region of the dolphin's cerebral cortex a considerable variety of reactions to acoustic stimuli is detected. As an example, Figure 40 shows, in the form of poststimulus histograms, the reactions of several neurons to uniform acoustic stimuli--clicks. Neurons can be detected with a short reaction of the phase type, lasting 30-50 msec (A). Neurons with an intermediate phase-tonic form of reaction respond with an intensive initial activation, which gradually falls in the course of 100-300 msec (B). Neurons with a typically tonic type of reaction respond with a prolonged (for hundreds of msec), slowly falling excitation to even a short click (C). Finally, neurons were encountered which responded to stimulus with a pause of silence lasting 200-300 msec, after which a burst of activity followed--postinhibitory activation (D). Therefore, in the auditory cortex of the dolphin's brain there is apparently a considerable variety of functional types of neurons which, as may be assumed, fulfill different functions in the processes of sensory analysis.

A study of the reactions of the cortical neurons to tonal transmissions showed that the reactions of the neurons depend on the frequency of the tonal signals used, and one may single out an optimum (characteristic) frequency for the given neuron, at which the neuron's response is maximal.

As an example we may examine the reactions of a neuron, presented in the form of poststimulation histograms in Figure 41. The reactions arise with the effect of tonal signals with frequencies of 30, 40 and 60 kHz. It can be seen that in the given neuron the reaction to a tone of 40 kHz substantially exceeds the reaction to tones of the adjacent frequencies. Unfortunately, the limited nature of the experimental material did not permit us to make a detailed study and comparison of the characteristic curves (relation of the reaction to the frequency of the tone) of different neurons.

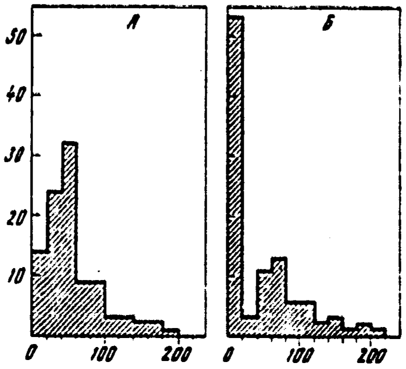


Figure 39. Histograms of Intervals Between Pulses for Various Types of Background Pulse Activity of Neurons of the Auditory Cortex of the Brain of a Porpoise Ph. phocoena

A--irregular activity; B--Grouped activity.
Along the axis of the abscissa--length of the intervals between pulses, in msec; along the axis of ordinates--number of intervals

The data presented, obtained in a microelectrode study of the activity of individual neurons of the dolphin's auditory cortex, as has already been emphasized, we regard as preliminary. Unquestionably the study of the activity of individual neurons may give quite important and interesting information on the characteristics of sensory analysis in the dolphin's auditory system as well. For this, however, such research must be developed on a considerably broader scale, which may be regarded as a task for future works.

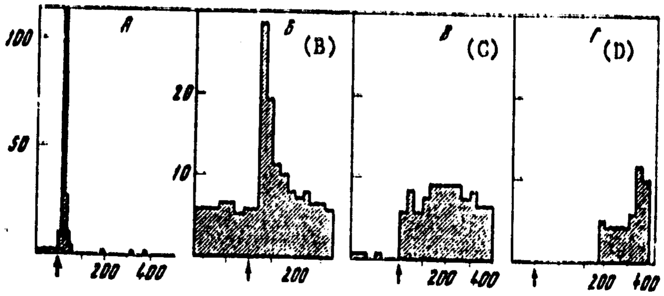


Figure 40. Types of Reactions of Neurons of the Auditory Cortex of the Brain of the Porpoise Ph. phocoena to Acoustic Clicks

Poststimulation histograms of various neurons. Each histogram is obtained by averaging 20 reactions of the neuron. A--phase reaction; B--phase-tonic reaction; C--tonic reaction; D--inhibiting reaction with postinhibiting output. Along the axis of the abscissa--time, in msec; along the axis of ordinates--frequency of pulse activity of neurons, in pulse/sec. The arrows indicate the moments of stimuli

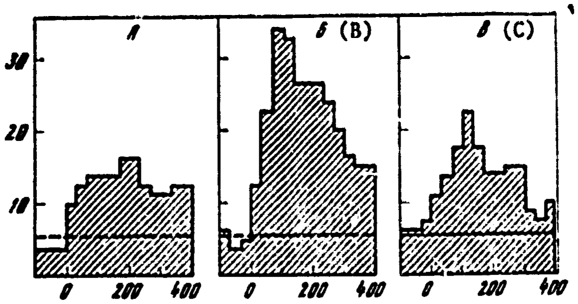


Figure 41. Reactions of Neuron of the Auditory Cortex of the Brain of the Porpoise Ph. phocoena to Tonal Acoustic Signals

Poststimulation histograms obtained by averaging 20 reactions. Along the axis of the abscissa--the time, in msec; along the axis of ordinates--frequency of pulse activity, in pulse/sec. Horizontal lines under the histograms denote the time of effect of the acoustic stimuli. Horizontal dotted lines--average level of background pulse activity of the neuron. Frequency of the tone: A--30 kHz, B--40 kHz, C--60 kHz.

2. Conditions for the Investigation of Evoked Potentials of the Auditory System

Substantial and important information on the mechanisms of sensory analysis may also be obtained by means of another classic method, which is more applicable when the number of animals used for the study is limited, as occurs in working with dolphins. This is the method of recording the summated bioelectric reactions to afferent stimuli--evoked potentials. At the early stages of investigation the use of this method proved unquestionably more useful and gave a large amount of information worthy of attention on the physiological mechanisms of processing sensory signals in the auditory cortex of the dolphins' brain (Popov, Supin, 1975, 1976 a, b).

The main part of the experiments was performed using bottlenose dolphins T. truncatus.

Leads were made from various sections of the auditory cortex. By preliminary probing we found the point of the cortex at which evoked potentials with considerable amplitude were recorded using acoustic stimulus. From this point we then made a chronic lead of the biopotentials for a long time, recording the reactions to the acoustic stimuli with systematically varied parameters. A considerable amount of information was obtained from each of the points of contact by this method.

Upon completion of the series of experiments, a coagulation marker was put in place with the aid of a diathermic coagulator. Morphological monitoring of the localization of the points of contact was subsequently made according to these markers.

At the time of the experiment, which lasted for several hours, the animal was placed in a tank measuring 3 X 0.5 X 0.4 meters, filled with sea water. After the experiment was completed the animal was released into a pen, where it was kept constantly. These recording sessions were repeated many times (usually daily) over a long period of time (up to several weeks or months) and made it possible to obtain a considerable amount of information from each of the implanted electrodes.

The acoustic stimuli were fed through piezoceramic transmitters from 1 to 6 cm in diameter, immersed in the water with which the experimental tank had been filled. The signals actuating the transmitters (tones, noises, clicks, etc.) were monitored directly at their input.

The animal's mobility in the tank was essentially limited. This made it possible, with the aid of a hydrophone, to measure the actual characteristics of the acoustic signal (form, intensity, etc.) immediately near the animal's head, which contributed to increasing the accuracy of the experiments.

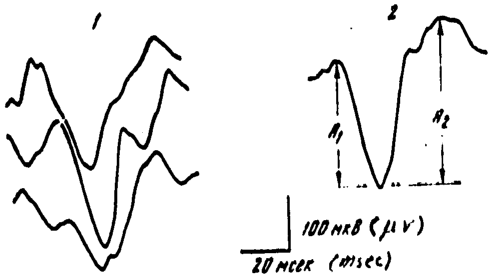


Figure 42. Responses of the Auditory Cortex of the Brain of a Bottlenose Dolphin to Acoustic Stimuli (Clicks)

1--examples of individual responses; 2--result of averaging 50 responses. The arrows (A_1 and A_2) show the measuring of the amplitude of the first phase and the overall amplitude of the response

The evoked potentials recorded were averaged (from 50-100 reactions) using the method of synchronous accumulation with the aid of an automatic electronic analyzer. The measurements of the amplitude and temporal characteristics of the evoked potentials were made according to these averaged evoked potentials (Fig. 42), and the numerical data thus obtained were used to plot graphs reflecting the relation of the parameters of the evoked potential to the characteristics of the stimulus. In a number of cases an additional averaging procedure was carried out: the graph, passing through a series of points, was approximated by a straight line. In these cases the position of the approximating straight line closest to the experimental points was found from equations of the lines of regression, i.e., if the approximating straight line is described by the equation

then

$$y = a + bx,$$

$$b = \frac{\Sigma (x - \bar{x})(y - \bar{y})}{\Sigma (x - \bar{x})^2}$$

and

$$a = \bar{y} - b\bar{x},$$

where x , y are the abscissa and ordinate of each point, and $\bar{x}$ and $\bar{y}$ -- the averages of all the values of x and y respectively.

3. Evoked Potentials at the Start and Stop of the Sound. Force Curves and Absolute Thresholds of Excitation of Evoked Potentials

One of the main characteristics of any analyzer consists of its absolute thresholds of perception and force characteristics--the relation of the reaction to the intensity of the stimulus. Therefore, the first stage in the electrophysiological study of the auditory complex of a dolphin's brain was also the determination of the absolute thresholds and force characteristics of the evoked potentials with different conditions of stimulus. For this purpose the responses of the auditory region of the dolphin's cerebral cortex were recorded at the start or stop of various sounds (noises, pure tones), as well as to acoustic clicks, by varying the intensity of the stimuli (Popov, Supin, 1976a).

Figure 43 shows the reactions of the auditory region of the cerebral cortex to acoustic clicks. As can be seen from the diagram, the temporal characteristics and form of the responses change little with a variation in the intensity of the stimulus; the amplitude of the responses is most obviously changed. Therefore, to obtain the force curves, the amplitude of the responses was measured at various intensities of the stimulus.

The amplitudes of various components of the response were measured. The basic ones were the measurement of the magnitude of the first phase of the response (from the isopotential line to the peak) and measurement of the overall amplitude of the response (from the peak of the first to the peak of the second phase), as shown in Figure 43. The results of the experiments showed, however, that both these values change in practically identical manner with a change in the characteristics of the stimulus; in particular, the force curves have an essentially identical form for both the amplitude of the first phase of the response, and for the overall amplitude of the response (Fig. 44). Therefore, in the future graphs were made that were plotted only according to the changes in the amplitude of the first phase of the responses.

Figure 44 shows the relation of the amplitude of the response to the intensity of the sound stimulus--a brief, broadband click (force curve). The intensity of the stimulus (acoustic pressure) is indicated according to the peak amplitude of the signal recorded through a contr. ı pickup hydrophone near the animal's head.

It can be seen that the force curve is divided into two clearly discernible sections. With relatively small intensities of the signal (up to 1 n/m^2), an increase in the amplitude of the response is observed with an increase in the intensity of the stimulus. With higher intensities of the stimulus (in Fig. 59, over 1-3 n/m^2), the increase in the amplitude of the response with an intensification in the stimulus ceases: the responses are essentially constant in magnitude (sometimes they are even somewhat reduced with high intensities of stimulus).

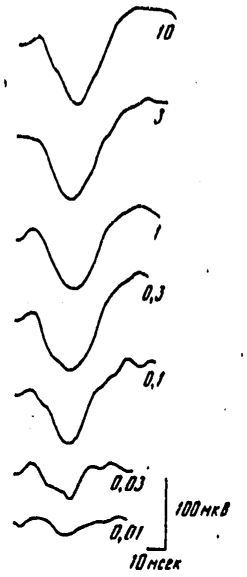


Figure 43. Responses of the Auditory Cortex of the Brain of a Bottlenose Dolphin to Acoustic Clicks of Varying Intensity

The intensity of the stimuli is indicated near the oscillogram (0.71 of the peak amplitude of the acoustic pressure, in n/m^2)

In the section of increase there is a virtually linear relation of the amplitude of the response to the logarithm of the acoustic pressure or power, i.e., to the intensity, expressed in decibels relative to a certain level.

Accurate determination of the thresholds of excitation of the evoked potentials is made difficult by the fact that very weak (near the threshold) responses are hard to single out from the background and to measure precisely even after the procedure of synchronous accumulation. It is possible, however, to make use of the fact that the amplitude of the response is in a linear relation to the logarithm of the intensity of the stimulus. If we extrapolate in a linear manner the sloping part of the force curve as far as the intersection with the axis of the abscissa, we obtain on it the value of the intensity at which a zero amplitude of response is expected (see Fig. 44). This intensity may be taken as the conditional estimate of the magnitude of the absolute threshold of excitation of the evoked potential for the given stimulus. As can be seen from Figure 44, the threshold value of the amplitude pressure of the acoustic click obtained in this way is about $3 \cdot 10^{-3}$ n/m^2.

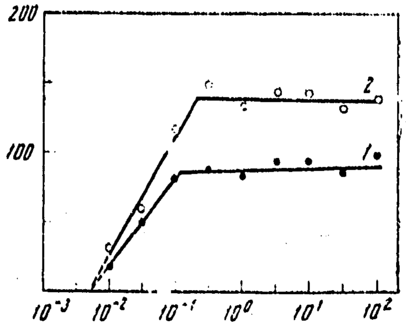


Figure 44. Relation of the Amplitude of Responses to Acoustic Clicks to the Intensity of the Stimulus

The same experiment as in Figure 58. Along the axis of the abscissa--the intensity of the stimulus (0.71 of the peak amplitude of the acoustic pressure), in n/m^2; along the axis of ordinates--the amplitude of the responses, in microvolts; 1--first phase; 2--overall

The method described was used to measure the thresholds of excitation of the evoked potentials with various forms of acoustic stimuli--not only with the effect of clicks, but also when starting and stopping noises and tones.

Figure 45 shows the force characteristics of the evoked potentials of the cerebral cortex of dolphins, recorded at the start of a broadband noise and of the pure tone optimal for the point being studied. The intensity of the noises and tones was measured according to the effective magnitude of acoustic pressure with a receiving hydrophone near the animal's head. Just as for the evoked potentials for the click, all the force curves shown in Figure 45 contain an initial sloping section and a plateau, and then on the sloping sections of the force curves there is essentially a linear relation of the amplitude of the response to the logarithm of the intensity of the stimulus. By extrapolating the sloping part of each curve to the intersection with the axis of the abscissa, it is possible to obtain an estimate of the absolute threshold of excitation of responses to the given form of stimulus.

Using noises or tones turned on for a relatively long time as the stimuli makes it possible to calibrate the stimuli with respect to the effective values of power or acoustic pressure. At the same time it is possible to make a comparison with the data on the absolute auditory sensitivity of dolphins obtained by different methods. In a number of cases the thresholds of excitation of the responses to starting the noise prove to be quite low and are close to the thresholds of absolute auditory sensitivity in dolphins. The force characteristics shown in Figure 45, A, 1 may serve as an example.

The threshold of excitation of the responses in this case is approximately equal to 10^{-3} n/m^2. There is a similar value, as was shown above, for the thresholds of absolute auditory sensitivity in bottlenose dolphins T. truncatus (Johnson, 1967; et al.) and in porpoises Ph. phocoena (Supin, Sukhoruchenko, 1974), with the action of the most effective audio frequencies.

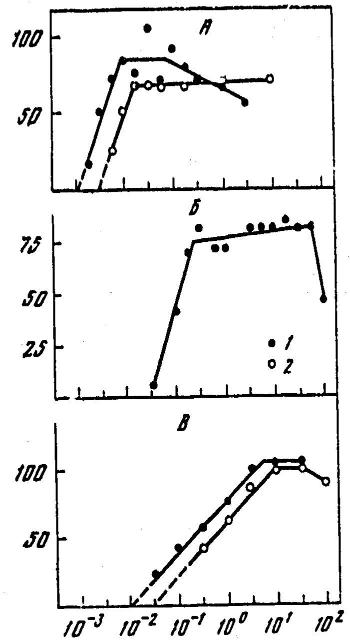


Figure 45. Relation of the Amplitude of Responses of the Auditory Cortex of a Bottlenose Dolphin's Brain to the Start of Noise and Tonal Acoustic Signals to the Intensity of the Stimulus.

A-C--different experiments and different points of recording: 1--responses to start of a broadband noise; 2--responses to start of a tone of an optimum frequency for the given point. Along the axis of the abscissa--the intensity of the signal (effective magnitude of acoustic pressure), in n/m^2; along the axis of ordinates--amplitude of the evoked potentials, in microvolts

As can be seen from Figure 45, A-C, the shape of the force curves may differ noticeably for evoked potentials recorded at different points of contact. The difference may pertain to the sensitivity and threshold of excitation of the evoked potentials and also to the steepness of the curve. For example, for responses to the same stimulus--the start of broadband noise--

the force characteristics of which are shown in Figure 45, A and B, the difference in the thresholds is about 30 db. The sloping part of the graphs in Figure 45, A and B occupy a segment of about 20 db, while in Figure 45, C it is about 60 db.

The fact that the thresholds of excitation of the evoked potentials in the auditory cortex of the dolphin's brain may essentially coincide with the absolute thresholds of auditory perception is extremely interesting. In actuality, one must take into consideration the fact that the evoked potentials are a reaction of a large number of neural elements. This means that the appearance of the evoked potential of even small amplitude, with near-threshold intensities of the stimulus signifies that these stimuli may activate a considerable number of neural elements, i.e., a large number of neurons in the dolphin's cerebral cortex have very low thresholds, close to the value of the absolute threshold of audibility in these animals.

Furthermore, the following fact indicates the existence of a large number of low-threshold neurons in the dolphin's cerebral cortex. As can be seen in Figure 45, A, the amplitude of the evoked potential very rapidly grows with an increase in the intensity of the stimulus, and achieves the maximum with the intensity exceeding the threshold by only 15-20 db. Further intensification of the stimulus no longer causes an increase in the amplitude of the response.

This obviously means that with a stimulus intensity of only 15-20 db above the threshold, practically all the neurons of the part of the cortex being studied that can be activated by the given stimulus have already been drawn into the reaction. Therefore, it may be concluded that the reaction thresholds of most of the neurons of this area of the cortex that respond to the start of the noise does not exceed by more than 15-20 db the absolute threshold of audibility for the dolphin.

Reactions to the starting and stopping of a pure tone had noticeably higher thresholds than reaction to the starting and stopping of a noise, even if the optimum frequency of the tone at which the greatest reactions with the lowest threshold were evoked was specially chosen. In Figure 45 A and C is an example of the force curves of the reactions of the same points of the cortex to starting a broadband noise (1) and tone of optimum frequency (2). The thresholds of excitation of reactions to the start of the noise may be 10-20 db lower than the threshold of reactions to the start of the tone. These data obviously may be regarded as evidence of the primary adaptivity of the points of the dolphin's auditory cortex studied to react to signals with a broadband spectrum.

4. Reaction of the Cortex to a Change in the Intensity of the Sound. Differential Thresholds According to Intensity

Evoked potentials in the dolphin's cerebral cortex may originate not only in response to the starting and stopping of a sound, but also in response to a change in the intensity of a constantly sounding signal (noise or tone). Experiments in which these reactions and their properties were studied were conducted in the following manner (Popov, Supin, 1976a).

The tone or noise of given intensity was heard constantly in the experimental tank. An increase or decrease in the intensity of the sound (momentary or with a regular front) to a certain magnitude served as the stimulus. The latent period and other temporal characteristics of the evoked potential were counted from the moment of change in the intensity of the sound. In the course of the experiment both the intensity of the constant (background) noise (ordinarily with a space of 5-10 db each) and the relative magnitude of intensification or weakening of the sound were varied. The following scale of magnitude of the change in intensity was ordinarily used: 1000, 300, 100, 30, 10, 3 and 1 percent of the magnitude of the acoustic pressure from the initial level of acoustic pressure.

The relation of the amplitude of responses to the intensity of the background noise and the amount of its change is shown graphically in Figure 46. It can be seen that with a reduction in the amount of change in intensity of the sound the amplitude of the responses drops. By continuing the sloping part of the curves to the intersection with the axis of the abscissa, we may obtain an estimate of the threshold value of the change in the intensity--the minimum value of the intensification or weakening of the sound (ΔI), at which the response originates.

The relative differential threshold, i.e., the minimum value of the relation $\Delta I/I$ (ΔI is the change in intensity, I -- the initial intensity), at which the response may be evoked is about 10% with respect to the level of the acoustic pressure for pure tones (0.6-0.8 db).

This value of the relative differential threshold, however, is observed only with sufficiently great background intensities of sound (in Figure 46,A with intensities of 0.3-1 n/m^2). If the background intensity of the sound is reduced and approaches the absolute threshold (threshold of origination of the responses to the starting and stopping of the sound), the relative differential threshold increases. If one analyzes this phenomenon, it is found that the minimal increase in intensity (ΔI), evoking the response, cannot be less than the value of the absolute threshold of excitation of the response to the starting or stopping. With low background intensities of the sound, approaching the absolute threshold, this is expressed in an increase in the relative differential threshold $\Delta I/I$. For example, in the experiment shown in Figure 46, the absolute threshold of the occurring of the response to starting was 10^{-2} n/m^2. With high background intensities (0.3-3 n/m^2), the relative differential threshold is about 10% with respect to the level of the acoustic pressure (0.7-0.8 db), since the change in intensity ΔI corresponding to this value, with the indicated background intensities is equal respectively to $3 \cdot 10^{-2}$ n/m^2, i.e., noticeably exceeds the threshold of excitation for the response to the starting. With a background intensity of 10^{-1} and $3 \cdot 10^{-2}$ n/m^2, however, the threshold change in intensity does not drop down below the value of the threshold of response to the starting and is over 10^{-2} n/m^2, which at these values of background intensity corresponds to the values of 1.5-5 db.

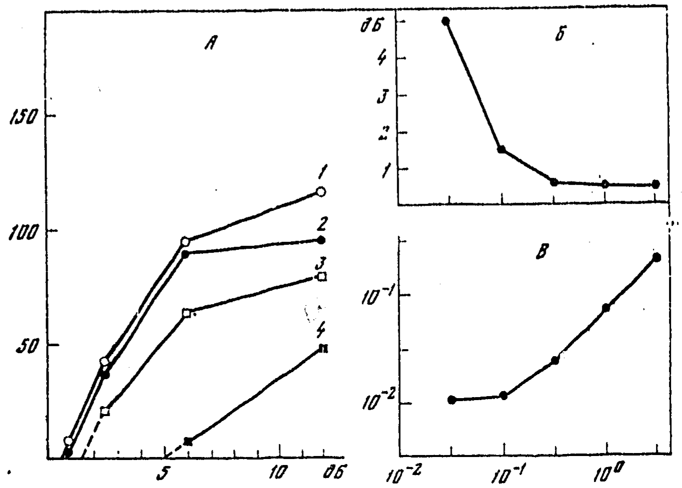


Figure 46. Characteristics of Responses of the Auditory Cortex of a Bottlenose Dolphin's Brain to a Change in Intensity of a Tonal Signal

A--relation of the amplitude of the responses to the amount of increase in the intensity of the sound. Along the axis of the abscissa--increase in acoustic pressure, in db; along the axis of ordinates--amplitude of the responses, in microvolts; 1--initial intensity of sound, 1 n/m^2; 2--0.3 n/m^2, 3--0.1 n/m^2, 4--0.03 n/m^2; B--relation of the differential threshold to initial intensity of the signal. Along the axis of the abscissa--the initial intensity of the sound, in n/m^2; along the axis of ordinates--the differential threshold, in db; C--relation of the differential threshold to the initial intensity of the sound. Along the axis of the abscissa--the initial intensity of the sound, in n/m^2; along the axis of ordinates--the threshold increase in acoustic pressure, in n/m^2

The conformances to principle described are well illustrated by graphs that show how the thresholds of responses to a change in intensity of the sound depend on the background intensity. Figure 46, B shows the threshold values $\Delta I/I$ at various background intensities of sound. The thresholds were found by extrapolation of the graphs shown in Figure 46, A. Figure 46, B shows the same data in a different form--as the relation of the threshold changes in intensity ΔI to the background intensity of the sound. It can be easily seen that with low background intensities (10^{-1}-$3 \cdot 10^{-2}$ n/m^2), the absolute threshold values of the change in intensity (ΔI) remain constant--they reach values close to the threshold of origination of responses to the start of the sound and do not drop lower. With higher intensities (0.3-3 n/m^2), the relative thresholds ($\Delta I/I$) become constant, and are established at a level of about 0.6 db.

The above-described experiments were performed using pure tones as the stimuli. Analogous measurements were obtained for broadband noise. The changes in the intensity of the noise result in the appearance in the cortex of analogous evoked potentials, thus changing, depending on the magnitude of the increase or decrease in the intensity of the sound. The threshold changes in intensity for noise, however, proved to be noticeably higher than the threshold changes in the intensity for the tone--30-50% (2-3.5 db).

It is possible, however, that the higher thresholds of change in intensity for noise are caused not by any specific reduction in sensitivity to this type of stimuli, but simply by the fact that in microintervals of time the amplitude of the noise is not stationary. This lack of stability in the amplitude may mask the moments of the changes in the average intensity of the noise, if these changes are not great. Therefore, the thresholds of reactions to a change in the intensity of the noise may prove to be raised.

5. Time Summation

A time summation is one of the important characteristics of an auditory system that determines the special features of perception of sounds of varying duration. This characteristic may also be studied using electrical reactions (evoked potentials) of the cerebral cortex.

The experiments were conducted as follows. The evoked potentials occurring in response to the sound transmissions (noises, tones) of varying duration were recorded. The relation of the amplitude of the responses to the duration of the transmission and intensity of the sound was studied.

The transmissions with a regulated transconductance of the front were formed by an electronic key controlled from a master oscillator. The length of the signals formed by the electronic key could be regulated within a broad range. Due to the reverberatory properties of the tank in which the studies were made, however, the length of the sound transmissions actually occurring in it could not be made shorter than 1 msec. Therefore, the capacity of the dolphin's auditory system for time summation was studied in our experiments for periods of time of at least 1 msec.

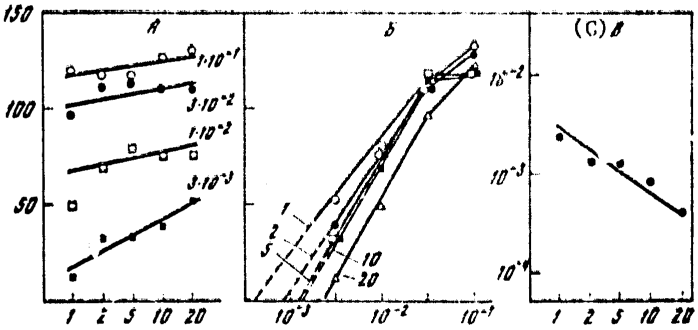


Figure 47. Effects of a Time Summation in the Auditory Cortex of the Brain of a Bottlenose Dolphin

A--relation of the amplitude of the evoked potentials to the duration of the noise transmission with varying intensities of stimulus. Along the axis of the abscissa--the duration of the stimulus, in msec; along the axis of ordinates--amplitude of the responses, in microvolts. Shown for each graph is the intensity of the noise--the effective value of the acoustic pressure, in n/m^2; B--the same data are presented as the relation of the amplitude of the response (along the axis of ordinates, in microvolts) to the intensity of the noise transmission (along the axis of the abscissa, in n/m^2) with varying durations of the transmission (indicated for each graph in msec); C--relation of the thresholds of excitation of the responses to the duration of the noise transmission according to the data of the same experiment. Along the axis of the abscissa--the duration, in msec; along the axis of ordinates--the threshold intensity of the noise, in n/m^2

Figure 47 shows the results of an experiment with a study of the reactions of the cortex to transmissions of a tone of varying duration. In the graphs of the relation of the amplitude of the evoked potentials to the duration of the sound transmission (Fig. 47, A), a clear increase can be seen in the amplitude of the responses with an increase in the duration of the transmission from 1 to 20 msec, which may be regarded as a phenomenon of time summation. It must be noted, however, that the observed increase in the amplitude of the responses is relatively small, i.e., in the range of durations studied (1-20 msec), the time summation is expressed relatively weakly.

The marked nature of the time summation depends on the intensity of the sound. If one compares the relation of the amplitude of the responses to the duration of the signal with varying intensities of the sound, it is discovered that an increase in the amplitude of the response with an increase in the duration of the sound transmission is shown better at low intensities. As can be seen from Figure 47, A, the graph of the relation of the amplitude of the responses to the duration of the sound transmission has the greatest steepness of the slope with a minimal ($3\cdot 10^{-3}$ n/m^2) intensity. At high sound intensities (in Fig. 47, A, to 10^{-1} n/m^2), the responses reach almost the maximum value at the lowest durations of the transmissions used (1 msec) and with a further increase in duration the amplitude of the responses changes little or not at all.

The process of time summation may be displayed not only in the increase in amplitude of the evoked potentials with an increase in the duration of the sound transmission, but also in the lowering of the thresholds of excitation of responses with an increase in the duration of the transmission. To reveal this effect, the thresholds of excitation of the evoked potentials were determined for sound transmissions of varying duration by means of the same method used in determining the absolute thresholds. By changing the intensity of the sound (with a given duration of the transmission), a force curve was constructed showing the relation of the amplitude of the response to the intensity of the stimulus (Fig. 47, B). At a certain section (in Fig. 47, B, from $3\cdot 10^{-3}$ to $3\cdot 10^{-2}$ n/m^2), the sloping part of the curve is well approximated by a straight line, the equation for which was calculated according to equations for the line of regression. The place where the curve intersects with the axis of the abscissa was regarded as the threshold of excitation of response to the sound transmission of the given duration (this point was also found by a numerical solution of equations of the line of regression). Using this method, graphs were plotted for varying durations of sound transmissions (Fig. 47, B): from 1 to 20 msec. As a result, the thresholds of excitation of the responses were determined in relation to the duration of the transmission.

Therefore, graphs may be plotted of the relation of the thresholds of excitation of the responses to the duration of the sound transmission (Fig. 47, C). It can be seen that with an increase in the duration of the sound transmission from 1 to 20 msec, a small but perceptible lowering takes place in the threshold of excitation of the response--in the experiment made, approximately by 15 db.

Experiments were described above in which it was possible to observe noticeable, even though not strongly marked, processes of time summation in the form of an increase in the amplitude of the responses and lowering of their thresholds with an increase in the duration of the sound transmission. Even this relatively weak time summation in the range of durations studied (1-20 msec), however, was by no means always observed. In a number of cases no noticeable changes in responses were observed at all when there was a change in the duration of the sound transmission in the indicated limits.

In addition, it should particularly be noted that noticeable process of time summation could be observed only when using transmissions of a broadband noise as the stimuli. This is also true of the experiment, the results of which were shown in Figure 47. When using pure tones, including those of the optimum frequency, as stimuli, no time summation could be observed with transmission durations over 1 msec.

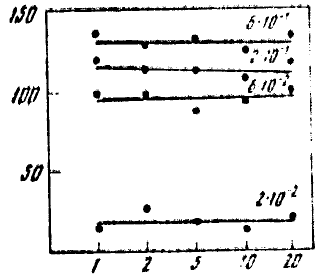


Figure 48. Absence of a Time Summation in the Auditory Cortex of a Bottlenose Dolphin's Brain With Stimulus by Tonal Signals

Stimulus--transmissions of a tone of 15 kHz of varying duration. Along the axis of the abscissa--duration of the transmission, in msec; along the axis of ordinates--amplitude of the responses, in microvolts. For each graph the intensity of the sound stimulus is indicated--the effective value of the acoustic pressure, in n/m^2.

The experiment, the results of which are shown in Figure 48, may be given as a characteristic example. In this experiment transmissions of a pure tone with a frequency of 15 kHz served as the stimuli. It can be seen that with not one of the intensities of stimulus used, including with the intensity close to the threshold, could a change in conformance with principle be observed in the amplitude of the evoked potentials that was related to the duration of the sound transmission. Accordingly, the thresholds of excitation of the evoked potentials essentially do not depend on the duration of the sound transmission. If force curves are plotted for each transmission duration, it can be seen that all the force curves intersect the axis of the abscissa at practically the same point, corresponding to a threshold of $1.5 \cdot 10^{-2}$ n/m^2.

Therefore, the processes of time summation within the range studied prove to be relatively weakly marked: with the effect of pure tones they could not be observed at all, and with the effect of noises, these processes, if they were observed, were only observed to a negligible extent. The data at our disposal so far does not permit us to say with certainty what the reason is for this phenomenon. Obviously, the processes of time summation in the dolphin's auditory system take place mainly in the course of shorter time intervals (less than 1 msec), so that, with our use of transmission durations of over 1 msec, the reactions had already almost achieved the maximum (and the thresholds of the reactions the minimum) values, and a further increase in the duration of the transmissions no longer or almost no longer led to a change in the magnitude of the reactions and thresholds.

On the other hand, it must be borne in mind that the method of evoked potentials does not permit a study of the processes of time summation with greater durations of the transmissions, since with a continuation of the transmission greater than the length of the evoked potential, its further increase can no longer affect the characteristics of the response. Therefore, in our experiments, the effect of a transmission duration up to 20 msec was studied, but longer transmissions were not used. At the same time, the possibility was not ruled out that in actuality, the reactions of the cortex could undergo a time summation in a broader range of durations.

In connection with this it is interesting to compare the data on the time summation obtained by us using the method of evoked potentials and by other authors by means of behavioral methods (Johnson, 1968b). Through the behavioral methods the time summation was detected in a very broad range of durations--from dozens of microseconds to seconds. With an increase in the duration of the sound transmission in these broad limits, the thresholds of reactions are quite substantially reduced--to a value in the order of 25 db or more. At the same time, however, a change in threshold by only 5 db or a little more is due to a change in the duration of the transmission of from 1 to 20 msec, which corresponds to the data obtained in our experiments. Therefore, it may be concluded that the method of evoked potentials in a limited range of durations yields results similar to the data of the behavioral experiments.

It is especially interesting that in our experiments the time summation in time segments over 1 msec could be observed better with the action of a noise than with the action of a pure tone, even if the frequency of the tone was selected as optimum with respect to the greatest magnitude of the reactions to starting it. A directly opposite phenomenon was described for cats (Zaboyeva, 1967); the longest time summation was observed with the action of a tone of a frequency optimum for the section being studied (characteristic frequency), but with the action of a noise the time summation was considerably less marked.

The long time of summation with the perception of a certain signal may be regarded as the suitability of the neural center being studied to analysis of this precise form of signal. This is indicated by the fact that the time summation is shown considerably better with the effect of a tone of the characteristic frequency than of other frequencies. In the dolphin, obviously, the optimum stimulus, at which the longest time summation is manifested, is not the tone of the characteristic frequency, but a noise with a sufficiently broad spectral band. This indicates a definite suitability of the dolphin's auditory system to analysis of broadband sound signals. We will recall that this was the conclusion drawn from the study of the absolute thresholds of excitation of the evoked potentials for the starting and stopping of a sound: with the action of a noise, the thresholds were substantially lower than with the action of tones.

In connection with this it is natural for the suggestion to arise of comparing the properties of the auditory system with the characteristics of the dolphins' echolocation apparatus: the locational pulses of bottlenose dolphins have a broadband spectrum. The possibility is not excluded that the features of the bottlenose dolphins' auditory system described reflect its suitability for analysis of location signals.

6. Depression of the Evoked Potentials With an Increase in the Duration of the Stimuli

The preceding section discussed only one effect observed with a change in the duration of the sound transmission: the lessening of the reactions (increase in amplitude and lowering of thresholds) with an increase in the duration of the stimulus. This effect is best shown with short durations and sound intensities near the threshold.

With intensities that substantially exceed the threshold intensity, the effect of the time summation is poorly marked or is lacking. Moreover, one may observe a directly opposite phenomenon, also of considerable interest: the depression of the evoked potentials of the cortex with an increase in the duration of the sound transmission.

Experiments in which this phenomenon was studied were made with the effect of noise transmissions lasting from 1 to 100 msec, formed by an electronic key. The duration of the transmission and the intensity (power) of the sound could be changed independently. Signals with an acoustic pressure level from 10^{-3} to 10^{2} n/m^2 were used.

The results of the two experiments conducted according to this program are shown in Figure 49, A and B. As can be seen from the diagram, at different points of the cortex the change in responses, depending on the duration of the transmission, may be different. In the experiment, the results of which are presented in Figure 49, A, with an increase in the duration of the sound transmission, only a slight increase is observed in the amplitude of the response at low sound intensities, i.e., a time summation. In the other experiment (Fig. 49, B), with an increase in the duration of the sound transmission, not only an increase, but also a reduction in the amplitude of the responses was observed.

The depression of the responses caused by increasing the duration of the sound transmission may be observed at various intensities of the sound signal. Moreover, depending on the intensity of the sound, as the duration of the transmission increases, at first a time summation may be observed, and only after that--a depression of the responses. The higher the intensity of the sound, the smaller the range of durations in which a time summation occurs. For example, when the sound intensity is $3 \cdot 10^{-1}$ n/m^2 (Fig. 49, B), the time summation is observed with an increase in the duration of the transmission to 10 msec, and only with an increase in the duration of the transmission to 20-50 msec does the amplitude of the response begin to drop. With a sound intensity of 1 n/m^2, the time summation is observed only up to 2 msec, and with an intensity of 3 n/m^2 and above there is no summation at all; with an increase in the duration of the sound transmission over 2 msec the depression of the responses immediately begins.

What causes the weakening of the responses of the auditory cortex with an increase in the duration of the sound stimulus? In order to answer this question, it must first of all be established whether the observed phenomenon is caused by any accompanying factors that appea' with a change in the duration of the stimulus. In particular, it should be noted that when sound transmissions of a great duration are used, separate reactions occur to the starting and stopping of the sound, while when short transmissions are used, both the starting and stopping of the sound may have an effect. It could be assumed that due to this the prolonged sound transmission evokes a weaker response (only at the start) than a short transmission (response immediately to starting and stopping).

An examination of the available data shows, however, that this circumstance is not the reason for the reduction in the responses described with an increase in the duration of the stimulus. A reduction in the amplitude of the responses may occur with durations of the stimulus (5 msec) in which the stimulus is even knowingly shorter than the latent period of the evoked potential occurring, and it is still not appropriate to speak of elimination of the stimulating effect of the moment of shut-off. With a long duration (10-20 msec), the amplitude of the response of the cortex is even more substantially reduced, but no breakdown is observed in the response to the components, which could be regarded as responses to the starting and stopping of the sound. Obviously, the effect of shutting off in these durations of the sound transmission is still too slight and makes no noticeable contribution to generating the summated evoked potential. Therefore, not the division in time of the effects of starting and stopping the sound, but the increased duration of the sound transmission should be the reason for the depression of the evoked potentials of the dolphin's auditory cortex observed.

There are no grounds for thinking that an increase in the duration of the sound transmission may lead to a decrease in its stimulatory effect. Therefore, it remains only to assume that, if a decrease in the responses of the cortex is observed with an increase in the duration of the sound stimulus, the reason for this is the inhibition arising in the auditory system, which actively depresses the responses of the cortex. Obviously, this inhibition is minimal with a brief duration of the sound stimulus, and increases with an increase in the duration of the stimulus, i.e., has the property of a time summation. A time summation of inhibition, as follows from the graphs given above, may develop in the course of at least tens of milliseconds. Moreover, in longer intervals, the time summation of the inhibition should predominate over the time summation of the excitation, as a result of which, with a certain duration in the sound transmission the amplitude of the reaction of the cortex ceases to increase and begins to decrease with a further prolongation of the transmission.

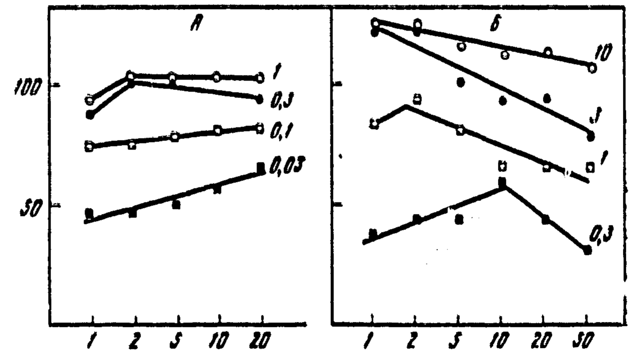


Figure 49. Different Variants of the Relation of the Amplitude of Evoked Potentials of the Auditory Cortex of the Bottlenose Dolphin to the Duration of the Stimuli (Noise Transmissions)

A--time summation; B--depression of responses with increase in duration of stimulus. Along the axis of the abscissa--duration of the stimuli, in msec; along the axis of ordinates--amplitude of responses, in microvolts. The intensity of the stimuli, in n/m^2, is indicated near the graphs.

In connection with the data presented, it is interesting to note that in the auditory system of bats and rats (inferior colliculus) neurons were discovered that reacted only to short signals, in the order of a few milliseconds (Grinell, 1963; Maruseva, 1969).

The inhibition revealed in the dolphin's auditory system was detected by the change in the evoked potentials in the auditory cortex. It is still impossible, however, to localize precisely the level of this inhibition (of the cortex proper or the underlying centers of the auditory system) according to the data presented. The evoked potentials of the cortex are an indicator that reflects the work of the entire underlying section of the auditory system from the receptors to the cortex, and the possibility is not excluded that the inhibition observed develops not in the cortex itself, but in one of the underlying auditory centers.

7. Dependence of the Evoked Potentials of the Auditory Cortex on the Characteristic Slope in the Front of the Sound Stimulus

When the electrical reactions of the cortex are evoked by the starting or stopping of the sound stimulus, an important parameter of the stimulus is the characteristic slope of its fronts--the time during which the intensity of the sound increases from zero to the maximum value or falls from the initial value to zero.

The evoked potential reflects the synchronous actuation of a large number of nerve elements, and for this there must be a clear-cut fixing of the moment of stimulus, which is possible only with a sufficiently steep front of build-up or drop in the intensity of the stimulus. Lengthening the front of the stimulus results in the entry of various nerve elements into the reaction being dragged out in time and the amplitude of the evoked potential occurring inevitably must decrease.

It can be shown, however, that the relation of the amplitude of the evoked potential to the steepness of the front of the sound stimulus may be determined not only by the synchronous nature of the actuation of the elements generating the evoked potential. For this we will examine the reactions of the auditory cortex of the dolphin's brain to starting a sound (broadband noise) with a varying steepness of the front.

Sound stimuli with a regulated steepness of the front were formed by an electronic key. The duration of the linearly building-up front changed from 0.1 to 100 msec.

As can be seen from Figure 50, the increase in duration of the front of the sound transmission causes a reduction in the amplitude of the evoked potential of the cortex. The drop in the amplitude of the responses with the increase in the duration of the front may take place at a varying rate. Cases are possible when the amplitude of the evoked potentials decreases relatively slowly in proportion to the increase in duration of the front of the stimulus (Fig. 50, A). Along with this, however, there may also be cases when the amplitude of the evoked potentials falls very rapidly, even with a slight increase in the duration of the front (Fig. 50, B). While starting up the noise with a front duration of 0.1 msec evokes a high-amplitude response, the stimulus with a front of 0.3-1 msec evokes a substantially weakened response, and stimuli with a front of 3 msec or more yield almost no responses.

It is vital that the reduction in the evoked potentials of the cortex occurs with durations of the front (from 1 to 3 msec) that are approximately of an order less than the duration and latent period of the evoked potential being recorded. No change was observed in the temporal characteristics of the responses to stimuli with a front of over 1 msec as compared with responses to stimuli with a shorter front.

In this situation the reduction in the amplitude of the evoked potentials cannot be explained only by the desynchronizing effect of the increase in duration of the front of the stimulus. It remains only to assume that the reduction observed in the evoked potentials reflects an actual weakening in the reactions of the auditory system to stimuli with a relatively long front. In this case the graphs of the relation of the amplitude of the evoked potentials to the duration of the front (Fig. 50, B) show that the sensitivity of certain elements of the dolphin's auditory system to the start of a sound depends on the rate of build-up in the intensity of the sound.

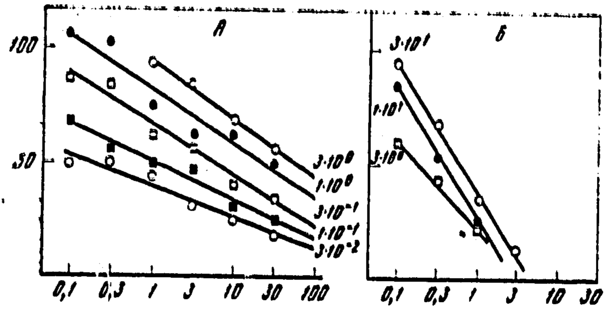


Figure 50. Relation of the Amplitude of Responses of the Auditory Cortex of the Brain of a Bottlenose Dolphin to the Duration of the Front of the Acoustic Stimulus (Noise Transmission)

A, B--different points of the cortex. Along the axis of the abscissa--the duration of the front, in msec; along the axis of ordinates--amplitude of the responses, in microvolts. The intensity of the noise (final value), in n/m^2, is shown near each graph.

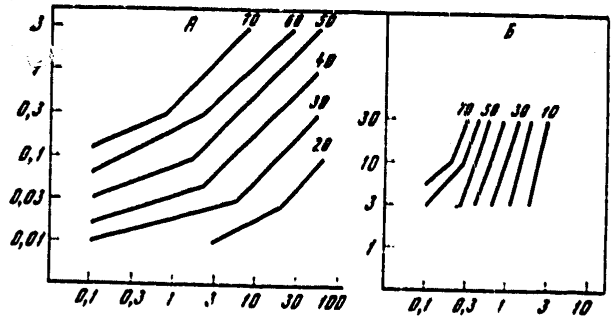


Figure 51. Relation of the Duration of the Front of the Stimulus (Along the Axis of the Abscissa, in msec) of the Final Intensity of the Noise (Along the Axis of Ordinates, in n/m^2) Necessary To Evoke Responses of Varying Amplitude

Same data as in Figure 65, A, B. The amplitude of the responses, in microvolts, is indicated near each graph.

In other words, it is obvious that the mechanisms of changes in the evoked potentials should be evaluated when their amplitude decreases considerably more slowly with an increase in the duration of the front of the sound stimulus, as was shown in Figure 50, A. Here responses of considerable amplitude are still recorded with an increase in the duration of the front of the stimulus to 30-100 msec, i.e., when the build-up time of the stimulus proves to be substantially greater than the duration of the evoked potential itself. In such cases, as shown in Figure 50, A, the reduction in amplitude of the evoked potential may be fully explained by the desynchronization of the afferent flow with an increase in the duration of the front of the stimulus.

The difference between the situations shown in Figure 50 is particularly graphically displayed if the same data are presented in another form--in the form of graphs showing at what ratio of the duration of the front and the final intensity of the noise responses of the same amplitude are obtained. In this case a set of graphs is obtained, each of which corresponds to a certain amplitude of the evoked potential (Fig. 51).

The data from the experiment that was shown in Figure 65, A are presented respectively in Figure 51, A. The most characteristic feature of these graphs is the fact that the right-hand part of each of them passes almost precisely at an angle of 45° to the axes of the coordinates, while the duration of the front and acoustic pressure are plotted along the axes of the coordinates on an equal logarithmic scale. This means that the amplitude of the response remains unchanged when a constant relation of the final acoustic pressure to the duration of the front is maintained, i.e., the amplitude depends only on the rate of build-up of the acoustic pressure, and remains constant with a constant rate of build-up of the acoustic pressure, regardless of the ratio of the duration of the front and the final acoustic pressure through which this rate is achieved.

In the left-hand part of the graphs presented in Figure 51, A, their slope decreases noticeably. This means that the reduction in the final acoustic pressure in this section can no longer be compensated for by a proportional reduction in the duration of the front of the stimulus. This may obviously be related to the fact that when the intensity of the sound approaches the threshold (which in this experiment was 10^{-3} n/m^2), the amplitude of the evoked potential should be affected not only by the build-up rate of the intensity of the sound, but also by the final intensity achieved.

The graphs shown in Figure 51, B, which present the same data as that in Figure 50, B, are of a completely different nature. The slope of these curves considerably exceeds 45°, i.e., the change in the duration of the gront affects the amplitude of the responses considerably more strongly than the proportional change in the final intensity of the sound. A situation that is at first glance paradoxical arises: with the same steepness of the front of the stimulus (build-up rate of the acoustic pressure), (as was done in other experiments described above), we obtain a point which may be regarded as the estimate of the threshold value of the frequency deviation--the minimum change in frequency that may evoke a threshold response.

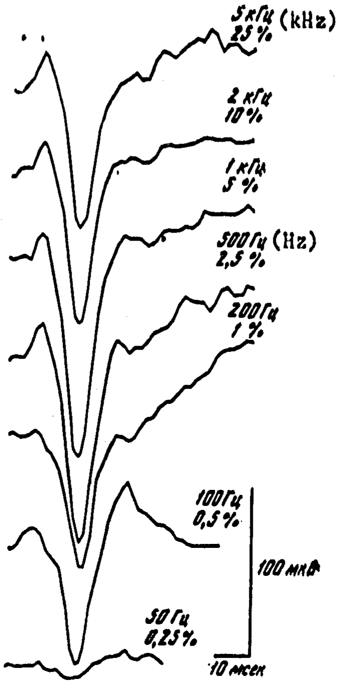


Figure 52. Responses of the Auditory Cortex of a Bottlenose Dolphin's Brain to a Change in the Frequency of the Tonal Sound

The initial frequency is 20 kHz. The change in frequency evoking the response is shown near each oscillogram

If we compare the values of the thresholds obtained in this way for the same point of the cortex with different values for the initial frequency of the tone, it can be seen that the threshold value of deviation ΔF, is approximately proportional to the initial frequency F, so that the threshold values of deviation may be more conveniently expressed in the form of the relative value $\Delta F/F$, which changes little with a change in the initial frequency. In the experiment, the results of which are shown in Figure 53, the threshold value of the frequency deviation is about 0.25% or somewhat more.

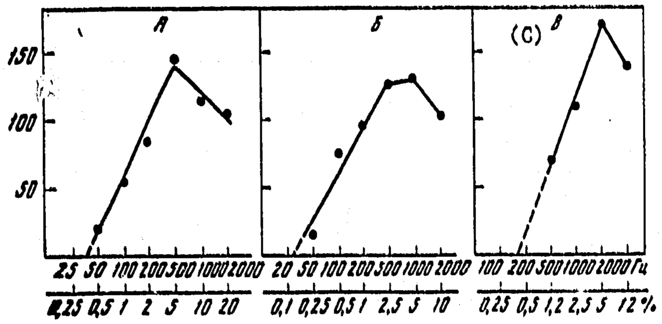


Figure 53. Relation of the Responses of the Auditory Cortex of a Bottlenose Dolphin to a Change in the Frequency of a Tone to the Value of the Frequency Deviation

A--initial frequency of the tone, 10 kHz; B--frequency of the tone, 20 kHz; C--frequency of the tone, 40 kHz. Along the axis of the abscissa--the value of frequency deviation (upper scale, in Hz, lower scale, in % of the initial frequency); along the axis of ordinates--amplitude of the responses, in microvolts

To a certain extent, however, the relative value of the threshold frequency deviation $\Delta F/F$ depends on the initial frequency F. In Figure 53, where data are given on the relation of the amplitude of the responses to the value of the frequency deviation at initial frequencies of 10, 20 and 40 kHz, it can be seen that the minimum relative value of the threshold frequency deviation is obtained with an initial frequency of 20 kHz; at the same time the threshold of excitation of the responses is less than 0.25%. With other initial frequencies--10 and 40 kHz--the threshold of excitation of the responses is somewhat higher: in a range from 0.25 to 0.5%. With any initial frequency, however, the threshold of excitation of the evoked potential does not exceed tenths of a percent. These values are close to the differential thresholds of discrimination for the frequency found for the auditory system of dolphins using conditioned reflex methods: these thresholds lie in the range from 0.1 to 0.5% (Jacobs, 1972); Supin, Sukhoruchenko, 1974; Thompson, Herman, 1975).

The shape of the graphs expressing the relation of the amplitude of the evoked potentials to the change in the frequency of the sound shows the range within which an increase in the amount of deviation leads to an increase in the amplitude of the response. As a rule, the responses reached the maximum with values of frequency deviation exceeding the threshold value 5-10-fold. With sufficiently low thresholds (from 0.1 to 0.2%), the response, therefore, may reach the maximum amplitude with values of frequency deviation in the order of 1-2%, as, for example, can be seen in Figure 53, B. In other cases, the amplitude of the responses rose with an increase in the deviation up to 2-5%; to a certain extent the stimulus that achieves a lower intensity in a shorter time evokes a greater response than the stimulus that achieves a greater intensity in a proportionally greater time. This phenomenon is obviously possible only if there is a special inhibiting mechanism that suppresses the responses to the stimuli with an increased duration of the front. It is interesting to note, in connection with this, that a study of the reactions of individual neurons in the inferior colliculus of the bat also showed the existence in this auditory center of neurons, the reactions of which depended substantially on the duration of the front of the build-up of the sound signal and could disappear even with a slight increase in the duration of the front (Vasil'yev, 1968).

8. Reactions of the Dolphin's Cerebral Cortex to a Change in Sound Frequency. Thresholds of Frequency Discrimination

It was discovered that in the auditory cortex of the dolphin's brain the evoked potentials may appear in response to a stimulus such as a change in the frequency of a constantly sounding tone. These reactions may be used to study the mechanisms of frequency discrimination in the dolphin's auditory system (Popov, Supin, 1976a).

Experiments in which a study was made of reactions to a change in the frequency of a tone were made in the following way. A constantly sounding pure tone of a selected frequency was fed through a transmitter. The intensity of the tone was usually chosen at a level of 40-60 db above the absolute threshold of excitation of the evoked potentials at the given frequency. A change (with a regulated slope of transition) in the frequency of the acoustic vibrations to a certain magnitude served as the stimulus. The temporal characteristics of the evoked potential brought about in this case (latent period, etc.) were counted from the moment of change in the frequency. In the course of the experiment both the initial frequency of the tone and the amount of change in the frequency (frequency deviation) were changed. The changes in amplitude of the evoked potentials depending on these two variables (initial frequency and amount of deviation) were studied.

Figure 52 shows examples of evoked potentials of the dolphin's cerebral cortex for a change in frequency of a tone with a varying amount of frequency deviation. It can be seen that the shape of the response changes little with a change in the amount of deviation, but the amplitude of the response changes substantially: it grows with an increase in deviation within certain limits. Therefore the basic value characterizing the relation of the evoked potentials of the cortex to the parameters of the stimulus in this case is also the amplitude of the response.

On the left sloping section of the graphs, the amplitude of the evoked potentials is essentially in a linear relation to the logarithm of the value of the frequency deviation. If we extrapolate this sloping section of the graph linearly to the intersection with the axis of the abscissa this value depends on the initial audio frequency F. These data may obviously be interpreted in such a way that in the main part of the neurons of the cortex that can respond to a change in the frequency of the tone the thresholds of these responses do not exceed 2-5%, and in some cases, with the use of optimum audio frequencies, the thresholds of most such neurons do not exceed 1-2%.

One must, however, take into consideration the fact that with a change in the frequency of the sound, an attendant change in its volume is inevitable --not only because of a certain lack of uniformity in the frequency response of the transmitter (which may to a considerable extent be corrected by instrument methods), but also because of the dissimilar sensitivity of the elements of the animal's auditory system to different audio frequencies. A check must be made as to whether the changes observed in the evoked potentials are the result of a change in the amount of frequency deviation or the result of the attendant changes in the intensity of the sound stimulus.

One of the variants of this monitoring is a comparison of the results obtained with different variants of the changes in the frequency deviation (Fig. 54). The frequency deviation in this experiment had various directions: an increase in the frequency of the sound from the initial one (Fig. 54, B, C) and a decrease in frequency (Fig. 54, A, D). In addition, the amount of deviation was changed by various methods: either the initial frequency of the tone remained unchanged, but the amount of deviation changed due to a different final frequency of transition (Fig. 54, A, C) or, conversely, the final frequency of transition remained unchanged, but the amount of deviation was varied, by changing the initial frequency (Fig. 54, B, D). It can be seen that with any of these methods of stimulation the curves of the relation of the amplitude of the responses to the amount of frequency deviation are mainly of a similar nature.

It may be assumed that the relation revealed between the amplitude of the evoked potentials and the amount of the frequency deviation is actually determined by mechanisms of frequency discrimination, and not by the effect of other factors. This is indicated, in addition to the control experiment described, by the relatively low value of threshold changes in the frequency that can evoke responses from the cortex (0.1-0.5%). With such small changes in the frequency it is difficult to expect quite large spurious changes in the volume of the signal, sufficient to cause evoked potentials in the cortex, especially since for the evoked potentials to appear there must be quite a substantial change in the intensity of the signal--as was shown above, about 1 db or a little less. Therefore, the described responses appearing with a change in the frequency of the sound may be regarded as responses precisely to the change in frequency, and not to the attendant change in volume, and the change in these responses, depending on the amount of frequency deviation, may be regarded as the reflection of the work of the mechanisms of frequency discrimination in the dolphin's auditory system.

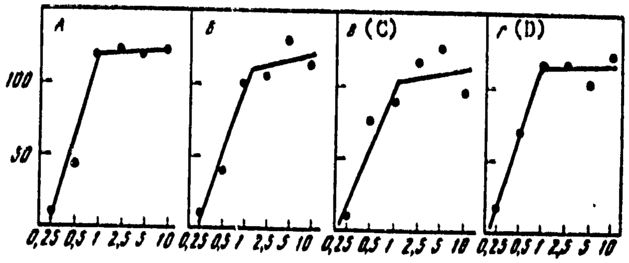


Figure 54. Relation of the Responses of the Auditory Cortex to a Change in Frequency to the Amount of Deviation With Different Variants of Stimulation

A--responses to a reduction in the frequency. The initial frequency is constant (20 kHz). The amount of deviation changes due to the final frequency of transition; B--responses to a rise in frequency. The final frequency of transition is constant (20 kHz). The amount of deviation changes due to the initial frequency; C--responses to a rise in frequency. The initial frequency is constant. A change in the deviation is due to the final frequency of the transition; D--responses to a reduction in frequency. The final frequency of transition is constant (20 kHz). The change in the deviation is due to the initial frequency. Along the axis of the abscissa--the amount of deviation, in % of the constant frequency of 20 kHz; along the axis of ordinates--the amplitude of the responses, in microvolts

Just like the responses to starting the sound, the responses to a change in frequency depend on the duration of the front of the stimulus--the segment of time in the course of which a transition takes place from one frequency to another. An increase in the duration of the front of the stimulus leads to a weakening of the responses to a change in frequency. The data from one of the experiments, in which a study was made of the relation of the responses to a change in frequency to the duration of the front of the stimulus are shown in Figure 55. It can be seen that with an increase in the duration of the front of the stimulus to 30 msec, the responses either considerably weaken or (depending on the amount of frequency deviation evoking the response) disappear completely.

The mechanism of the observed weakening of the responses with an increase in the front of the frequency deviation becomes clearer if the same data are presented in the form of graphs that show the ratios of the amount of frequency deviation and front of the stimulus at which responses of the same amplitude are evoked (Fig. 56, A). In this case it can be seen that with values of the deviation from 2 kHz (10%) and above, the graphs proceed at an angle of practically 45° to the axes of the ordinates, if the amount of deviation and duration of the front of the stimulus are plotted along the corresponding axes on an identical logarithmic scale. This means that the amplitude of the response remains unchanged with a constant relation between the amount of deviation and the duration of the front of the stimulus, i.e., the amplitude of the response depends only on the rate of change in the frequency $\Delta F/t$. With lower values for the frequency deviation, however (from 1 to 2 kHz in Fig. 56,A), the slope of the curves changes. This indicates that the reduction in the amount of frequency deviation in this range causes a considerably sharper reduction in the amplitude of the response than a proportional increase in the duration of the front of the stimulus. Obviously, in this range the amplitude of the response is determined not only by the rate of change of the frequency, but also by the actual value of the frequency deviation, which is fully in accordance with the data presented above: in the range of deviation values of 5-10% the amplitude of the responses depends on the amount of the deviation.

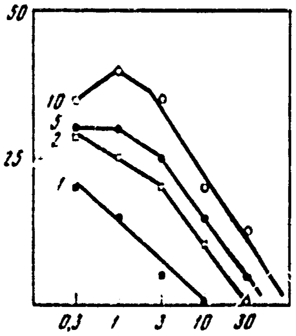


Figure 55. Relation of the Responses of the Cortex to a Change in the Audio Frequency to the Steepness of the Front of the Signal

Stimulus--an increase in the frequency of a continuously sounding tone. The initial frequency of the tone is 20 kHz, and the increase in frequency is indicated in kHz at each curve. Along the axis of the abscissa--the duration of the front (time in which the frequency increases linearly from the initial value to the final), in msec; along the axis of ordinates--the amplitude of the responses, in microvolts.

Therefore, a relation of the responses to a change in frequency to two factors is discovered. In the range of amounts of deviation up to 2-5% the amplitude of the response depends primarily strictly on the amount of the deviation, and with greater changes in the frequency (over 10%)--on the rate of change of the frequency. By using the data on the relation between the amplitude of the responses and the amount of deviation and front of the stimulus (see Fig. 56, A), a graph may be plotted that shows how the amplitude of the responses to greater values of frequency deviation depends on the rate of change in the frequency (see Fig. 56, B).

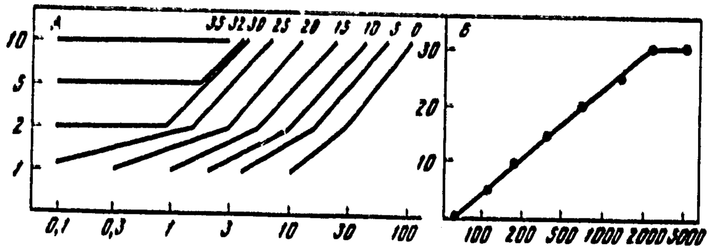


Figure 56. Relation of the Deviation in Frequency Necessary to Evoke a Response of a Given Amplitude on the Duration of the Front of the Signal (A) (Same Data as in Figure 70)

Along the axis of the abscissa--duration of the front, in msec; along the axis of ordinates--finite value of the deviation in frequency, in kHz. The amplitude of the responses is indicated for each graph in microvolts; B--relation of the amplitude of the responses to the rate of change in the frequency of the sound according to the data of the same experiment. Along the axis of the abscissa--the rate of change in the frequency, in kHz/sec; along the axis of ordinates--amplitude of responses, in microvolts.

Everything that has been said, however, refers only to the sections of the cortex in which responses can be recorded to sufficiently small, as described above, changes in frequency--in the order of percents and fractions of a percent. At a number of points of contact in our experiments the evoked potentials of the cortex were not detected with slight changes in the frequency: either it was completely impossible to obtain responses to a change in the frequency of the sound, or the responses occurred only with very great changes in the frequency (by tens of percents or by several times). In the latter case the change in frequency should obviously inevitably be accompanied by a change in the volume of the sound and by a click at the moment of transition, which also could not be a factor directly evoking the response. In these cases there are no grounds for evaluating the evoked potentials occuring as responses to a change in the frequency of the sound.

Therefore, it was revealed that different sections of the cortex possess a varying ability to react to a change in the frequency of the sound: at some points, with a change in the frequency of the sound, distinct responses with low thresholds occur, and in others it is not possible to record responses that could with any certainty be considered to be a reaction to a change in frequency.

9. The Reaction Capacity of the Auditory Cortex for Reproduction With Paired and Rhythmic Stimuli

Repeated sound stimuli (clicks) evoke responses with reduced amplitude if the interval between the testing and preceding (conditioning) stimulus is sufficiently small. A small reduction in the amplitude of the testing responses is observed at intervals in the order of 500 msec and less, but at these intervals the amplitude of the testing responses still differs little from the control. A substantial weakening in the responses (less than 50% of the value of the response to an individual stimulus) takes place at intervals between clicks of 5-30 msec and less. The response to the testing stimulus, however, is not fully depressed, and is quite clearly manifested even at short intervals (20 msec and less) in which the testing response is superimposed on the conditioning one (Fig. 57). By making a pointwise subtraction of the curve of the response for a paired stimulus, it is possible to obtain in pure form the shape and magnitude of the response to the second stimulus. In this case it is discovered that the response to the repeated stimulus, of a small, but nonetheless perceptible magnitude, arises at intervals between the stimuli up to 10 msec. The data obtained in this way make it possible to construct a graph that reflects the relation of the amplitude of the testing evoked potential to the interval between the conditioning and testing stimuli (Fig. 58).

The relatively weak depression of the reactions of the cortex to repeated sound stimuli is also manifested when rhythmic stimuli are used--series of clicks, repeated with different frequencies. In this case the capacity of the evoked potentials of the cortex to track with sufficiently high frequencies the presentation of acoustic clicks is detected.

The characteristic picture of the evoked potentials occurring with the presentation of series of clicks is shown in Figure 59. With a sequence of clicks with a frequency of up to 7-10 pulses/sec (in Fig. 59, 8 pulses/sec), the responses can still be little distinguished from the responses to individual stimuli. At higher frequencies (in Fig. 59 from 16 to 25 pulses/sec), the response to the second click of the series already proves to be substantially reduced as compared with the first, but the amplitude of the responses to the subsequent clicks in the series is restored to a considerable extent (working-in effect). It may be noted that the "working in" or the responses to the rhythmic clicks is connected with the change in the ratio between the various components of the response: the amplitude of the primary positive oscillation is reduced, but the amplitude of the slower secondary components is increased, since they become the basic components of the rhythmic reaction. In Figure 59 this process is seen at frequencies of stimulation of 16 and 25 pulses/sec; apparently, it also takes place at higher stimulus frequencies, but the individual components of the responses in this case are not easily discernible.

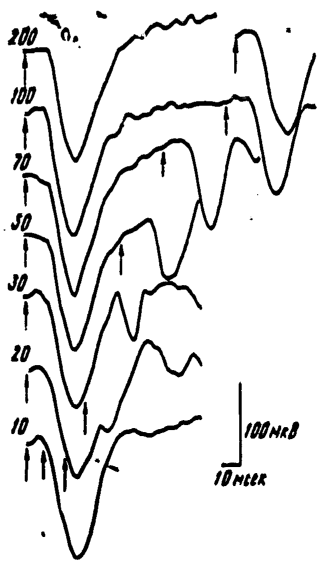


Figure 57. Responses of the Auditory Cortex of the Brain of a Bottlenose Dolphin to Paired Acoustic Clicks

Moments of stimuli (clicks) are marked with arrows under oscillograms. The intervals between the clicks are indicated in msec. The intensity of the clicks (0.7 of the peak level of the acoustic pressure) is 1 n/m^2

At stimulation frequencies of over 20-40 pulses/sec (in Fig. 59 40 pulses//sec and over) the amplitude of the rhythmic reaction already decreases noticeably. A reaction, although weak, however, is still discernible at frequencies in the order of 100 pulses/sec (in Fig. 59, 90 pulses/sec).

The depression of the evoked potentials of the dolphin's cerebral cortex with repeated sound stimuli should be acknowledged as relatively shallow. Studies made using different analyzers of other animals and man show that with paired stimuli it is possible to have a deep depression of responses to the testing stimuli in the course of hundreds of milliseconds after the conditioning stimulus. The oscillograms given above show that the dolphin's cerebral cortex may generate separate responses to acoustic clicks repeated at an interval of 10-20 msec, which is considered to be a relatively high (for the cerebral cortex) temporal resolution.

Evoked potentials obtained with other methods of stimulation are subject to similar conformities to principle. Reactions to repeated changes in the frequency of the sound may be discussed as an example.

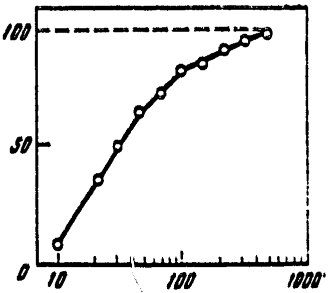


Figure 58. Relation of the Amplitude of Responses to Repeated Acoustic Clicks to the Interval Between the Clicks (Same Data as for Figure 57)

Along the axis of the abscissa--the interval between paired clicks, in msec; along the axis of ordinates--the amplitude of the response to the second click, in % of the amplitude of the response to the first click.

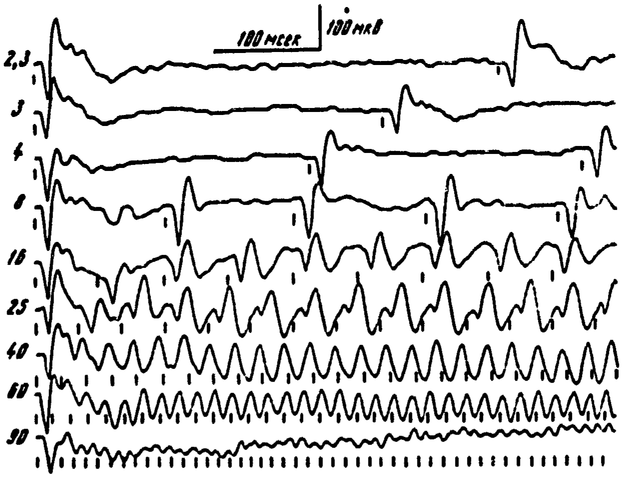


Figure 59. Responses of the Auditory Cortex of a Bottlenose Dolphin's Brain to Rhythmical Series of Acoustic Clicks

Moments of stimuli (clicks) are marked under the oscillograms. The frequency of the rhythmic stimulation, in pulses/sec, are indicated near the curves. The intensity of the clicks (0.7 of the peak level of the acoustic pressure) is 1 n/m^2

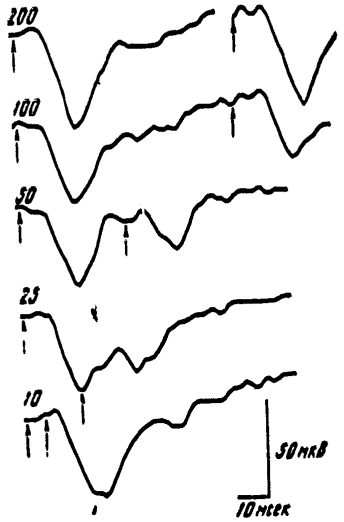


Figure 60. Responses of the Auditory Cortex of the Brain of a Bottlenose Dolphin to Repeated Changes in the Frequency of a Continuously Sounding Tone.

The moments of stimuli are indicated by the arrows under the oscillograms. The first stimulus is a change in the frequency from 35 to 30 kHz, and the second stimulus is a change in the frequency from 30 to 25 kHz. The numbers at the left are the intervals between the stimuli, in msec

In these experiments the change in the frequency of the sound from the initial value to a certain new one (Fig. 60, from 35 to 30 kHz) served as the first stimulus. The second stimulus was a new change in the frequency of the sound in the same or the reverse direction (Fig. 60, a further lowering of the frequency from 30 to 25 kHz). The interval between the first and the second shift in the frequency could be varied within a wide range. As can be seen from the oscillograms given, with long intervals between the shifts in frequency, the amplitude and shape of the first and second responses do not essentially differ. With a reduction in the interval to 100 msec and less the amplitude of the second response decreases, but a noticeable response to the second stimulus is still observed at an interval of 25 msec, and by subtracting the response to the individual stimulus from the response to the paired stimuli, one may single out the response to the second shift in frequency even at an interval of 10 msec.

The excitability curves (relation of the amplitude of the second response to the interval between the stimuli) are practically identical even when changes in the frequency in the same direction serve as the first and second stimulus, just as when changes in the frequency in opposite directions serve as the first and second stimulus (Fig. 61).

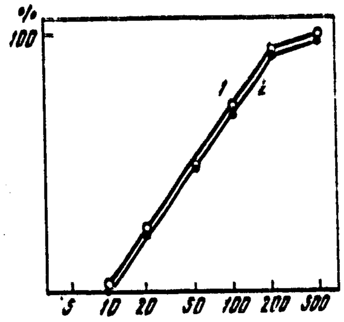


Figure 61. Relation of the Amplitude of Responses to Repeated Changes in Frequency to the Intervals Between the Stimuli

Along the axis of the abscissa--the interval between the stimuli, in msec; along the axis of ordinates--amplitude of the responses, in %. 1--first stimulus--a change in frequency from 35 to 30 kHz, second--from 30 to 25 kHz; 2--first stimulus--a change in frequency from 35 to 30 kHz, second--from 30 to 35 kHz

10. Reactions of the Auditory Cortex to Sound Stimuli Delivered Against a Background of Interference

The interference-suppressing feature of the dolphin's auditory system, including the receiving part of the locational apparatus, represents an extensive and important separate problem. This section discusses only one of the aspects of this problem: the relation of the electrical reactions of the dolphin's cerebral cortex to the effect of interference masking the basic signal.

A very simple variant of experiments with masking can be recording the responses to clicks delivered against the background of a continuously active noise, with varying ratios of intensity of the stimulating click and masking noise. The results show that with a sufficient intensity of the masking noise, comparable with the intensity of the testing signal, a reduction occurs in the amplitude of the evoked potentials of the auditory cortex, and with a sufficiently high intensity of the masking noise--their full depression. The results of this experiment are shown in graphic form in Figure 62 for two intensities of the testing click as the relation of the amplitude of the evoked potentials to the intensity of the masking noise. It can be seen from the graphs that if the masking noise is 10-15 db weaker than the click, the depression of the evoked potentials essentially does not occur, and the amplitude of the reactions does not differ from the amplitude of the control (without masking noise) response to a similar click. An increase in the intensity of the masking noise results in a drop in the amplitude of the testing reaction, and complete depression of the reaction is observed when the intensity of the noise rises 12 db above the intensity of the testing signal (with both intensities of the click used). When the acoustic pressures of the click and the noise are equal, a depression of approximately 50% was observed in the evoked potentials of the cortex.

Adding a click (which, just as the noise, has a broadband spectrum) to the noise constantly in effect may be regarded as a short-term increase in the intensity of the noise to a certain magnitude. Therefore, it is interesting to compare the results of experiments with the clicks sent out against a background of noise and experiments with the recording of the reactions to a change in the intensity of the noise. If one considers that the threshold of masking is a noise 12 db higher than the instantaneous power of the click, this means that the threshold of excitation of the response is an increase in the power of the noise of 1.06-fold, or by 0.25 db (if an increase in the noise of 10 db above the signal is taken as the threshold of masking, we accordingly obtain the threshold increase in the power of 1.1-fold, or by 0.4 db). These values are noticeably lower than the estimates that were obtained for the thresholds of excitation of the noise (2.5-3.5 db) and even lower than the thresholds for a change in the intensity of the tones (0.6-0.8 db). It is possible that this difference is related to the fact that the spectrums of the testing click and the masking noise are different, even though both of them are broadband. The lack of coinciding of the maximums of the spectral power for the testing and the masking signals may weaken the effectiveness of the masking.

The importance of the coinciding of the spectral characteristics of the testing and masking signals for effective masking is graphically displayed in a comparison of experiments with the masking of the click with noise and masking of the click with a pure tone. When the pure tone is used as the masking sound, a reduction in the amplitude of the responses to the clicks may also be observed, down to their complete depression (Fig. 63). In contrast, however, to the masking with noise, in the latter case much greater intensities of the masking tone are required. As can be seen from Fig. 63, given the equality of the power of the testing click and the masking tone no perceptible reduction in the amplitude of the responses to the clicks is noted at all, and for complete suppression of the responses to the clicks, an intensity of the masking tone is required that exceeds the intensity of the click by 35 db (addition of a click, the power of which is 35 db less than the power of the constantly sounding tone, corresponds to increasing the intensity of the sound 1.0003-fold, or by 0.013 db). This may indicate that the auditory system of dolphins singles out with high selectivity the broadband signals of the click type against a background of tonal signals.

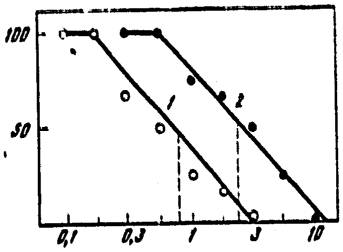


Figure 62. Masking With Noise the Responses to Clicks of the Auditory Cortex of the Brain of a Bottlenose Dolphin

Intensity of the click that is the stimulus (0.71 of the peak level of the acoustic pressure) 0.8 n/m^2 (1) and 2.5 n/m^2 (2). Along the axis of the abscissa--the intensity of the masking noise (effective acoustic pressure), in n/m^2; along the axis of ordinates--amplitude of responses, in % of the magnitude of the responses in the absence of a masking noise. The vertical dotted lines indicate the levels of acoustic pressure equal to the intensity of the click-stimuli (0.8 and 2.5 n/m^2).

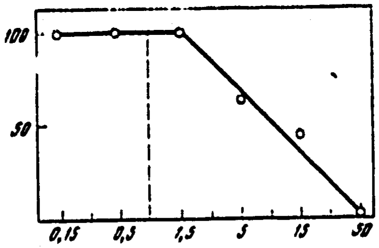


Figure 63. Masking With a Tone the Responses to Clicks of the Auditory Cortex of the Brain of a Bottlenose Dolphin

Intensity of the click is 0.8 n/m^2. Along the axis of the abscissa--the intensity of the masking tone (effective acoustic pressure), in n/m^2; along the axis of ordinates--the amplitude of the responses, in % of the magnitude of the responses in the absence of a masking tone. The vertical dotted line indicates the level of acoustic pressure equal to the intensity of the click-stimulus.

11. Functional Differentiation of Various Sections of the Auditory Cortex and Various Components of the Evoked Potentials

As was shown, in different sections of the auditory cortex of the dolphin's brain, evoked potentials varying in form and duration may be recorded, which obviously attests to varying functional properties of the sections of the cortex generating these potentials. Singled out in the auditory cortex of the brain of a bottlenose dolphin were the following basic components of evoked potentials, which may be recorded either separately or mutually superimposed: 1) responses with a latent period of 7-8 msec and the time to the peak--10-15 msec; 2) responses with a latent period of 12-13 msec and the time to the peak 20-30 msec; 3) slow oscillations with longer latent periods (see Figure 10). The polarity of the different components of the evoked potential may be positive or negative, depending on the localization of the point of contact.

The difference in the characteristics of the evoked potentials is not always unequivocally related to the features of the anatomic arrangement of the sections of the cortex generating them. Often complex evoked potentials could be recorded that contained several components, i.e., at the same point of the cortex, oscillations differing in shape and temporal characteristics appeared. Most often observed was the superimposing of a late oscillation, with the time to the peak 50-60 msec, on earlier components of the evoked potential. Therefore, components, different in form, of the electrical reaction of the cortex to sound stimulus may be generated by the same or at least closely positioned sections of the cortex.

The temporal characteristics of the evoked potentials recorded in the given point of the cortex were usually a permanent characteristic of this point and did not depend on the method of stimulation (click, starting or stopping a sound, frequency or amplitude modulation), if only the stimulus used could evoke a noticeable reaction.

In some cases the impression may be created that a change in the characteristics of the stimulus results in a change in the form of the responses. More detailed analysis shows, however, that in these cases only a relative change takes place in the magnitude of the various components of the reaction that can be generated by the given point of the cortex. In this case the general form of the evoked potential changes, but the temporal characteristics of each of the components remain unchanged. Some of these situations are discussed in particular below.

As was already noted in describing the relation of the magnitude of the evoked potentials of the cortex to the parameters of the stimulus (intensity, duration, etc.), the nature of the change in the responses being recorded at various points of the cortex may differ substantially. The differences may be observed even between responses of the same type being recorded at various points of contact. Especially natural are the differences for these features between responses of a different form and the duration, i.e., responses of various types.

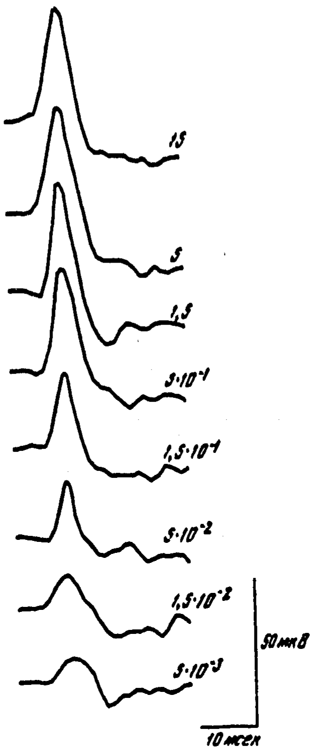


Figure 64. Short-latent Responses of the Auditory Cortex of the Brain of a Bottlenose Dolphin to Sound Stimuli (Clicks)

The intensity of the clicks (0.71 of the peak level of the acoustic pressure) in n/m^2 are indicated near the oscillograms

We will discuss in greater detail the differences between various types of evoked potentials of the cortex with respect to a simple, but essential feature such as the relation to the intensity of the stimulus. The material presented above mainly pertained to the most frequently encountered responses with a latent period of 12-13 msec and a time to the peak of 25-26 msec, i.e., responses of type II in accordance with the classification proposed above (Chapter 2). It was shown (see Fig. 45) that the range of intensities within the limits of which the amplitude of the evoked potentials of this type increases with an intensification of the stimulus is different, but lies within a range of 20-50 db.

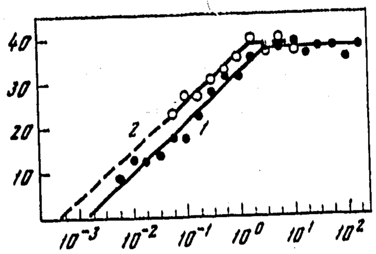


Figure 65. Relation of a Short-Latent Response of the Auditory Cortex (see Fig. 64) to the Intensity of the Stimulus

Along the axis of the abscissa--the intensity of the stimulus (level of the acoustic pressure), in n/m^2; along the axis of ordinates--the amplitude of the responses, in microvolts; 1--responses to clicks (intensity of the stimuli is measured as 0.71 of the level of the peak acoustic pressure); 2--responses to starting a broadband noise (intensity is measured according to the effective magnitude of the acoustic pressure)

Early responses with a latent period of 7-8 msec and the time to the peak about 15 msec (responses of type I) behave somewhat differently. These responses change relatively slowly in amplitude in proportion to a change in the intensity of the stimulus. At the same time, the threshold of the reactions proves to be quite low: responses that are slight, but clearly singled out from the background, can be easily recorded at levels of acoustic pressure somewhat higher than 10^{-3} n/m^2 (Fig. 64). The relation of the amplitude of these evoked potentials to the logarithm of the intensity of the stimulus is well approximated by a sloping straight line with a plateau following (Fig. 65), with the sloping section of the graph occupying quite a large range of intensities--about 70 db, and the threshold of excitation of the responses to the acoustic click, estimated according to the point of intersection of the curve with the axis of the abscissa, may be about 10^{-3} n/m^2 (Fig. 65, 1). The force characteristics of the same evoked potential, obtained in response to starting the noise, has a similar slight slope (Fig. 65, 2). Just as for the other responses, the threshold of excitation of the reaction to starting the noise, estimated according to the effective acoustic pressure of the latter, is approximately 10 db lower than the threshold of excitation of the response to the click.

Therefore, in the evoked potential of type I (with the time to the peak about 15 msec), occurring in response to both a click and the starting of a prolonged sound, the force characteristics have considerably less slope than with the type II potential evoked later.

This difference in the relation of the two types of evoked potentials of the cortex to the intensity of the stimulus is also observed when both these responses are recorded simultaneously at the same point of the cortex, i.e., are generated by closely positioned sections of the cortex. An example of this is the experiment shown in Figure 66. In this experiment, with relatively high intensities of stimulation, the basic component of the evoked potential recorded is the oscillation with the time to the peak 26 msec, i.e., a response of type II. It reaches the maximum magnitude with stimulus intensities of 0.3 n/m^2 and higher, and with a reduction in the intensity to 0.17 n/m^2 and lower, the amplitude of this oscillation drops rapidly. This rapid drop in the amplitude of the response, however, is observed only with a reduction in the intensity of the stimulus to 0.1 n/m^2, after which the remaining small evoked potential, with a weakening of the stimulus, is reduced very slowly.

From the oscillograms in Figure 66, however, it can be seen that the response remaining with a reduction in the intensity of the stimulus to 0.1 n/m^2 and below is not identical to the response occurring with higher intensities of stimulus: it reaches the peak 17 msec after the moment of stimulus instead of 26 msec with the higher intensities. Moreover, the transition from one form of response to the other takes place not by means of a gradual change in the duration of the evoked potential, but by substituting one potential for the other. It can be seen in Figure 66 that the temporal characteristics of the response do not change at all with a change in the intensity of the click from 1.7 n/m^2 to 0.3 n/m^2 (peak at the 26th millisecond), just as they do not change with a change in the intensity from 0.1 to 0.006 n/m^2 (peak at the 17th msec). The only form of evoked potential with intermediate temporal characteristics (with an intensity of 0.17 n/m^2) may be explained by the mutual superimposing of the two oscillations of the evoked potential.

If the relation of the two components of the evoked potential to the intensity of the stimulus is presented in graphic form (Fig. 67), the difference in their characteristics can be clearly seen. One component of the evoked potential rapidly increases to the maximum with an intensification in the stimulus, but has a higher threshold (curve 1). The other component (curve 2) changes considerably more slowly, depending on the intensity of the stimulus, but the estimate of the threshold of excitation of this component turns out to be quite low--about $10^{-3} n/m^2$.

Another example of the differences in the functional properties of the various components of the electrical reaction of the auditory cortex is the interrelation between the late slow oscillation of the potential (peak at the 50th millisecond) and the earlier response. In many cases the slow oscillation is recorded following the primary evoked potential, and the response to the sound stimulus is formed by the mutual superimposing of these two components (force characteristics and thresholds, capability of occurring in response to the starting and stopping of the sound, etc.) differ considerably. As a rule, the slow component proves to be more resistant to a weakening in the intensity of the stimulus and to other changes in the conditions of the stimulus.

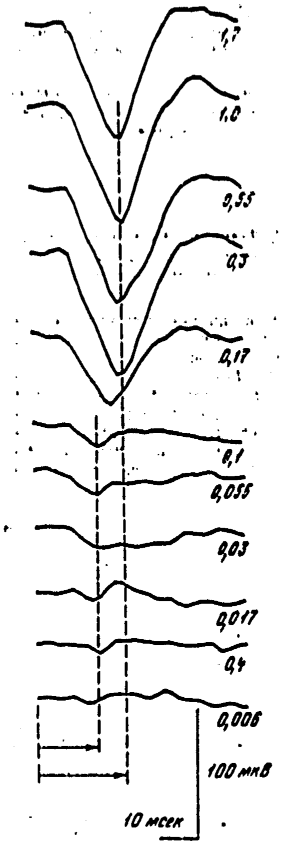


Figure 66. Simultaneous Recording at a Single Point of a Short-Latent Response of the Auditory Cortex With the Time to the Peak 17 msec and of a Response With the Time to the Peak 26 msec.

Stimulus--acoustic click. The intensity of the stimuli (0.71 of the peak level of the acoustic pressure) is shown near the oscillograms in n/m^2. For convenience in comparison, vertical dotted lines are made through the peaks of the responses with different temporal characteristics; the time to the peak of the two types of responses (17 and 26 msec) is indicated by the arrows below

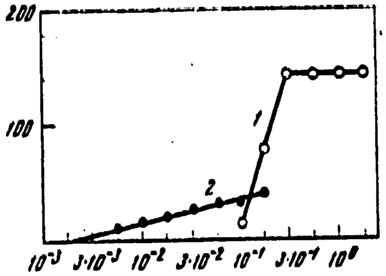


Figure 67. Relation of the Responses of Two Types Recorded at the Same Point (see Fig. 67) to the Intensity of the Stimulus

Along the axis of the abscissa--the intensity of the acoustic stimulus (click), measured as 0.71 of the peak value of the acoustic pressure, in n/m^2; 2--response with the time to the peak--17 msec

A typical situation is given in Figure 68, where it can be seen that the slow oscillation with a peak of about 50 msec has a lower threshold than the relatively early oscillation with a peak at the 25th msec. The slow oscillation is clearly marked when the intensity of the stimulus is 0.2 n/m^2, while the early response at this intensity is practically nonexistent. The early component of the response occurs with intensities of 0.6-2 n/m^2, even though the slow wave at these intensities still remains the dominant component. Further intensification of the stimulus leads to an increase in the amplitude of the early component of the evoked potential, while the slow oscillation at these intensities ceases to increase and even begins to be depressed (60 n/m^2). Therefore, all the force characteristics of slow oscillation prove to be shifted to the area of lower intensities as compared with the force characteristics of the early component (Fig. 69).

The varying properties of the fast and slow components of the evoked potential are also clearly discovered in a comparison of the responses to different forms of stimulus, for example, to starting and stopping a sound. Figure 70 shows the responses of the same points of the dolphin's cerebral cortex to the starting (A) and stopping (B) of a sound--a broadband noise. In this case the start of the noise evokes a response containing both components described: both the rapid response with a peak at the 25th msec and the slow wave. Stopping this sound, however, evokes only a slow wave, and in this case the more rapid component is not observed. Therefore, at this point of the cortex, the slow component of the evoked potential may occur in response to both the starting and the stopping of the sound, and the more rapid component--only in response to its starting.

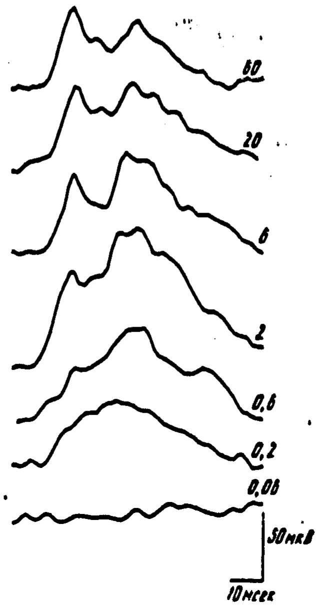


Figure 68. Primary and Slow Components of an Evoked Potential of the Auditory Cortex of the Brain of a Bottlenose Dolphin with Varying Intensities of the Sound Stimulus (Click)

The intensity of the click (0.71 of the peak acoustic pressure), in n/m^2 is shown near the oscillograms

Therefore, the varying components of the evoked potentials are characterized by varying sensitivity to the acoustic stimuli and by a varying capacity of occurring with the starting and stopping of a sound and with other effects. This difference, as follows from the data given above, occurs even between the components of the evoked potential that are recorded from the same electrode, i.e., between components that are generated by cortical structures that are relatively close.

These differences are particularly possible between responses that are recorded from various parts of the cortex--at various points of contact. From the data presented above it can be seen that it is possible to have substantial differences between the responses recorded at various points of contact for the thresholds of excitation, for the steepness of the relation of the amplitude of the response to the intensity of the stimulus (see Fig. 45), for the sensitivity to the lengthening of the front of the stimulus (see Fig. 50), etc. Not only the actual fact of the difference in the characteristics of the responses recorded at various points of contact is of interest, however. As it turned out, the characteristics of the stimuli at which it is possible to obtain at a certain specific point of contact evoked potentials of maximum amplitude are grouped into definite complexes, similar to the complexes of features in certain natural stimuli, with which the auditory system of dolphins may have a connection (Popov, Supin, 1978).

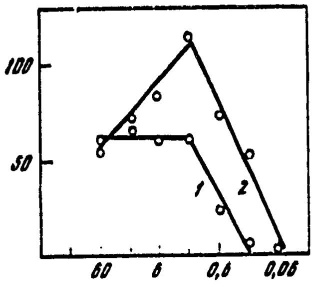


Figure 69. Relation of the Amplitude of the Primary and Slow Components of the Evoked Potential (see Fig. 68) to the Intensity of the Acoustic Stimulus (Click)

Along the axis of the abscissa--the intensity of the stimulus, in n/m^2; along the axis of ordinates--the amplitude of the components of the response, in microvolts; 1--primary component; 2--slow wave

As an example we will compare the properties of the responses of two especially selected points of the cortex (two points of contact). The relation to a number of characteristics of acoustic stimuli was quite fully studied for these responses. Some of the graphs shown above (see figs. 49, 50) were plotted according to the responses of these precise points of the cortex. We will conditionally designate them as points of contact A and B. The localization of the points of contact is shown in Figure 71. Both points of contact are localized in the auditory projectional area of the cortex (middle super-Sylvian gyrus) in the same animal. At both points responses are recorded that are similar in form with the latent period about 15 msec, i.e., responses of type II. Nevertheless, with a change in the series of characteristics of the sound stimuli, the responses of these two points behave completely differently, as is shown schematically in Figure 71.

Spectrum of the signal: point A reacts to both broadband signals (noises, clicks) and to narrowband (pure tones). Point B reacts only to broadband signals (clicks or noises) and essentially does not react to pure tones.

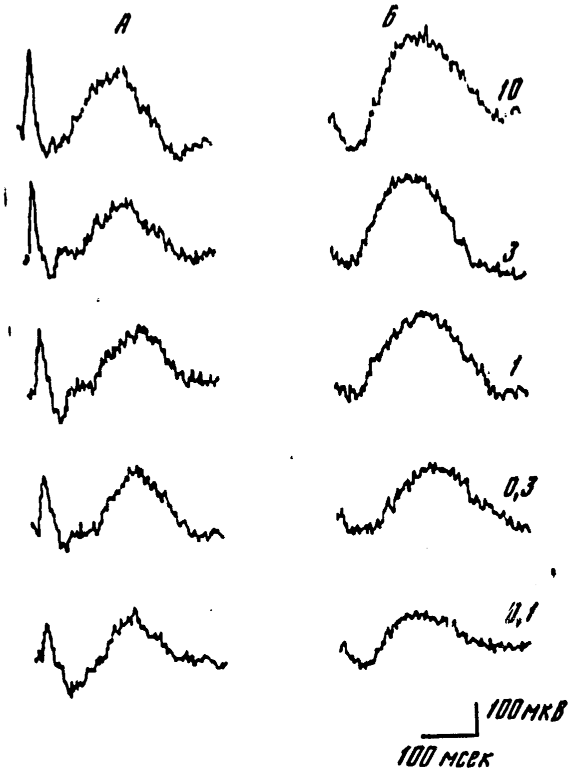


Figure 70. Varying Manifestation of Primary and Slow Components in Responses of the Cerebral Cortex of a Bottlenose Dolphin to the Starting (A) and Stopping (B) of Acoustic Stimulus (Noise)

Near the oscillograms--intensity of the noise, in n/m^2

Duration of the signal: with an increase in the duration of the signal the responses of point A are not depressed, or a certain capacity for time summation is even detected (see Fig. 49, A). The responses of point B are noticeably depressed with an increase in the duration of the signal (see Fig. 49, B).

Duration of the front of the signal: the responses of point A are relatively weakly depressed with an increase in the duration of the front, so that the responses of considerable amplitude can still occur with a duration of the front in the order of 100 msec and more (see Fig. 50, A). The responses of point B drop sharply even with a negligible increase in the duration of the front of the signal, and practically disappear when the duration of the front is about 10 msec (see Fig. 50, B).

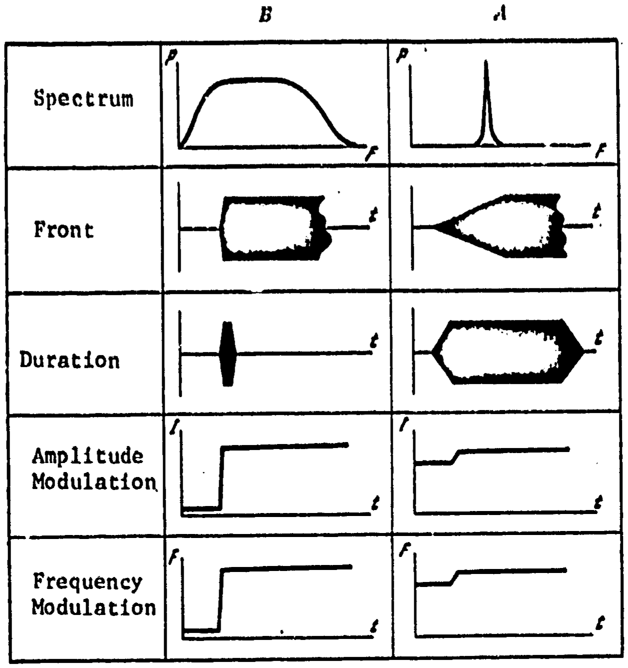


Figure 71. Characteristics of Acoustic Stimuli Optimum for Evoking Reactions at Different Points of the Auditory Cortex of a Bottlenose Dolphin's Brain

Explanation in text

Amplitude modulation: the responses of point A, which may appear with the start of a pure tone, may also occur with a change in its intensity. The responses of point B do not occur with a change in the intensity of the pure tone or appear only with large drops with short fronts in which the signal is accompanied by a click at the moment of transition.

Frequency modulation: responses of point A may occur to relatively small changes in the frequency of the signal. The responses of point B may occur only with the large drops and sharp changes in the frequency of the signal that are accompanied by a click at the moment of transition.

Consequently, point A may react not only to broadband, but also to narrowband (pure tone type) signals, including relatively long ones slowly changing in amplitude and frequency. Point B reacts only to short narrowband signals with a steep front, i.e., signals of the click type. It is, however, precisely from these complexes of characteristics in bottlenose dolphins that two large groups of acoustic signals are differentiated: communicational and locational. The communication signals of the bottlenose dolphins are relatively narrowband (whistle-type) signals with amplitude and frequency modulation. The location signals are short broadband clicks. This fact leads to the assumption that the cerebral cortex of dolphins has a spatial demarcation of the structures that are specialized for perception and analysis of communicational and locational signals.

There has not yet been an opportunity of establishing whether some sort of orderliness exists in the arrangement of the sections of the cortex with different functional properties and if it exists, what its nature is. The actual possibility of such a spatial division of the sections with different functional properties, however, deserves attention and further study.

12. The Presence of Specialized (Detector) Elements in the Auditory System

One of the fundamental theories of modern physiology of sensory systems is the concept of the existence in the sensory systems of specialized (detector) neurons, which as the result of a certain organization of the excitatory and inhibiting communications arriving at them react selectively to specific, sometimes quite complex characteristics and properties of afferent stimuli. This area of sensory physiology is studied most fully and in greatest detail for the visual system of various animals (see, for example, the survey: Supin, 1974; and others). Some types of detector neurons, however, for example the neurons that react selectively to a certain direction in the change in intensity or frequency of a sound, are also described in auditory centers (Whitfield, Evans, 1965; Gersuni, Vartanian, 1973; Suga, 1973; and others).

A study of the specialized detector neurons is also very interesting, particularly because these studies may show directly which features of afferent stimuli are used by the appropriate analyzer of a certain specific animal to analyze and identify signals. Therefore it would be important and interesting to ascertain which detector systems exist in the dolphin's acoustic analyzer and which features of the acoustic stimuli are singled out by these dector elements and are used to analyze acoustic signals--communicational and locational.

Detailed investigation of the detector elements in sensory systems unquestionably requires a microelectrode study of the activity of individual neurons, since only in this case can the detector properties of the neuron be revealed and an attempt made to analyze the mechanisms that form these properties. As was pointed out at the beginning of this chapter, however, microelectrode studies of individual neurons in the dolphins' cerebral nerve centers have so far proved to be unacceptable due to the limitedness of the material.

This does not mean, however, that a study of the detector elements in dolphins' sensory systems is impossible until widescale introduction of microelectrode studies made with these animals. A number of preliminary, but worthy of attention, data pertaining to this question may also be obtained indirectly--in a study of the summarized electrical reactions of the brain and by other methods. Studies of the detector elements in the human visual system are significant in this respect. Merely with the aid of psychophysiological experiments and recording from the surface of the head the summary electrical activity of the brain it was shown that there are many classes of detector elements in the human visual system, and some properties of these elements were studied (see survey: Supin, 1974).

It appeared expedient to make a study of this type for the sensory systems of dolphins as well, primarily for the auditory system. The results of a number of these experiments, directed toward ascertaining the specialized detector elements in the dolphin's auditory system (Popov, Supin, 1976b) are presented below.

Elements, discriminating changes in the frequency of an acoustic signal. Shifts in the audio frequency may be one of the most important characteristics of dynamic acoustic signals. It has been shown that in the auditory centers of a number of animals there are specialized detector neurons that react to a change in the audio frequency, sometimes only to a certain direction (raising or lowering) of change in frequency (Whitfield, Evans, 1965; Suga, 1972; and others). Therefore, it is interesting to establish whether such neurons are present in the auditory system of dolphins and what their properties are.

The possibility of the appearance in the auditory cortex of the brain of dolphins of reactions (evoked potentials) to a change in the frequency of a sound (see above) is in accordance with the idea of the existence in the auditory system of dolphins of neurons that are selectively sensitive to shifts in the audio frequency. These data, however, cannot yet serve as proof of the existence of such specialized neurons, since the appearance of reactions to a shift in the frequency may be related not only to activation of specialized detector neurons, but also to other mechanisms. For example, it may be assumed that reactions to a change in frequency occur because in a very simple way, as to the start of a noise, the neurons are actuated for which the final frequency of transition is optimum, and the initial--not optimum. As at the stopping of a sound, a reaction to a change in frequency may be shown by the neurons for which the initial frequency was optimum and the final frequency of transition proves to be not optimum. In order to verify whether specialized detectors, sensitive to a shift in the audio frequency, take part in the generations of reactions of the dolphin's auditory cortex to a change in frequency, special experiments are necessary.

One of the forms of experiment which can serve as an indication of the existence of specialized detectors of the direction of a shift in an audio frequency is presented in Figure 72. Used here as the stimulus is a specific form of signal such as a change in the direction of the shift of the audio frequency. The frequency of the tonal acoustic signal at first changes linearly--builds up or diminishes--in the course of a certain segment of time, and then the direction of the change in the frequency of the sound changes to the opposite (Fig. 72, B).

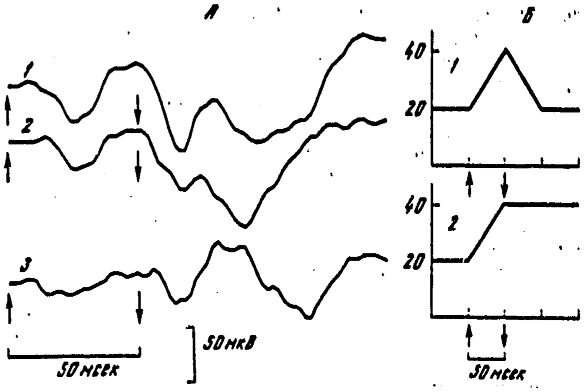


Figure 72. Response of the Auditory Cortex of a Bottlenose Dolphin's Brain to a Change in Direction of the Shift in Frequency of a Sound

A--oscillograms; B--diagrams illustrating the nature of the change in the time of the frequency of a continuously sounding tone (along the axis of the abscissa--the time; along the axis of ordinates--the frequency of the tone, in kHz); 1--frequency of the tone builds up in the course of 50 msec from 20 to 40 kHz. Then the direction of the change in frequency changes jumpwise to the opposite, and the frequency of the tone begins to diminish at the same rate; 2--frequency of the tone builds up in 50 msec from 20 to 40 kHz and remains at this level; 3--the difference in oscillograms A, 1 and A, 2. Under the oscillograms are indicated the moments when the build-up of the frequency of the tone begins (arrow upwards) and when the direction of the shift in frequency changes to the opposite or the shift in frequency ceases (arrow downwards)

In this case the following reasoning may be performed. If the reaction to the change in frequency is evoked only by the fact that new neurons are drawn in, for which the changed audio frequency is characteristic, there should be no noticeable response to the change in direction of the shift in the frequency: after all, after the moment of the change in the direction, the frequency of the tonal signal assumes primarily the same values that it had before that moment, and neurons with new characteristic frequencies should not be drawn into the reaction.

If, however, the reaction to the shift in frequency is caused by the activeness of specialized detector neurons, then a reaction of the cortex may occur in response to the change in the direction of the shift of the audio frequency, since different detectors may be selective for different directions in the shift of the frequency, and after the moment of the change in the direction of the shift in frequency a new group of detector neurons may join in.

The results of the experiments show that at some (not at all) points of contact distinct reactions may be recorded to a change in the direction of the shift in the audio frequency (Fig. 72, A, 1). At least two clearly marked responses may be singled out on the oscillogram: to the beginning of the change in the frequency of the tonal signal (peak 25 msec after the beginning of the stimulus) and the response to the change in direction of the shift in frequency with a brief latent period (peak 16 msec after the moment of change in the direction of the shift of the audio frequency).

For comparison, the reaction was shown of the same point of the cortex to a stimulus in which the element of change in the direction of the shift in frequency was eliminated. The frequency of the tonal signal changes at the same rate and in the course of the same segment of time as in the preceding case, but after that does not begin to change in the opposite direction, but remains unchanged (Fig. 72, B, 2). The reaction to this stimulus (Fig. 72, A, 2) in its initial section contains a similar response to the beginning of the change in frequency as oscillogram 1. But instead of a high-amplitude response to the change in the direction of the shift in frequency, only a considerably lesser response is observed to cessation of the shift in frequency (it may be regarded as an analog of the response to stopping for the neurons sensitive to a change in frequency).

If a pointwise subtraction is made of curve 2 from curve 1 (see Fig. 72,A), it is possible to obtain the difference curve 3, which presents in clearer form the response to the change in direction of the shift in the audio frequency. It can be seen that the response obtained has considerable magnitude. The data obtained are therefore well in agreement with the idea of the existence in the dolphin's auditory system of specialized nerve elements that react to certain directions in the shift in frequency of acoustic signals.

In some cases a simpler and more direct method can successfully demonstrate the presence in the auditory cortex of the dolphin's brain of specialized elements that discriminate change in frequency. As was shown above, a change in the frequency of a continuously sounding tone may evoke in the dolphin's auditory cortex a clearly marked evoked potential. The main difficulty lies in showing that this reaction is generated precisely by the neurons sensitive to a shift in frequency, and not to the starting and stopping of the sound, since a rapid change in the frequency of the tone may be regarded as stopping the tone of one (the initial) frequency and simultaneous starting of a tone of a different frequency.

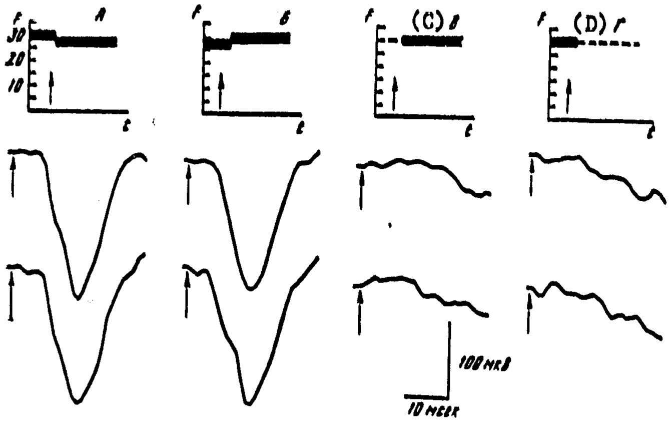


Figure 73. Comparison of Responses of the Same Point of the Auditory Cortex of the Brain of a Bottlenose Dolphin to a Change in the Frequency of the Tone and to the Starting and Stopping of the Tone

A--responses to a change in the frequency of a continuously sounding tone from 30 to 27 kHz; B--responses to a change in the frequency of the tone from 27 to 30 kHz; C--responses to starting a tone of 30 kHz of the same intensities; D--responses to stopping the same tone. From top to bottom: diagram illustrating the nature of the stimulus (along the axis of the abscissa--the time, along the axis of ordinates--the frequency of the tone, in kHz); responses with the intensity of the tone 50 n/m^2; responses with the intensity of the tone 15 n/m^2. The arrows indicate the moments of stimuli--changes in the frequency of the tone, starting or stopping the tone.

This difficulty proved to be unexpectedly easy to eliminate, at least for certain points of the auditory cortex of the dolphin's brain. It was discovered that at some points of contact it was possible to record clearly marked reactions to relatively small changes in the frequency of the tone with the essential absence of reactions to starting or stopping tonal signals in the same range of frequencies and with the same intensities.

An example of reactions of such a point of the cortex is presented in Figure 73. The point of the cortex studied generates clearly marked evoked potentials in response to a change in the frequency of the tone, and with responses of maximum amplitude, shown in Figure 73, A and B, they occur with a 7-10% shift in the frequency. Essentially identical evoked potentials occur in response to both a reduction in the frequency (Fig. 73, A, shift of frequency from 30 to 27 kHz) and to a rise in it (Fig. 73 B, shift of the frequency from 27 to 37 kHz). Neither starting nor stopping a tone in this section of the frequency range, however, evoked noticeable reactions.

Figure 73, C and D, shows the starting and stopping of a tone of 30 kHz; other frequencies did not evoke noticeable effects either. This means, obviously, that the reaction to a shift in the frequency of a constantly sounding tone cannot be explained, for example, as a response to starting a tone of 30 kHz and stopping a tone of 27 kHz, or vice-versa.

It must be noted that the following explanation is possible for the appearance of reactions to a shift in the frequency in the absence of responses to starting and stopping tones of the same frequencies. With a rapid shift in the frequency, in a short interval of time it passes through a series of values from the initial value to the final one--an expansion of the signal spectrum takes place that causes a spatial summation of the excitations in the canals of the auditory system discriminating adjacent frequencies. It is due to this spatial summation that signals with a broadband spectrum can evoke reactions more efficiently than narrowband tonal signals.

Even if the mechanism for the appearance of responses to a shift in frequency is precisely of this type, however, this cannot be an argument against the assumption of the existence in the dolphin's auditory system of elements that react to shifts in frequency. It is precisely the spatial summation that may be the natural mechanism creating the sensitivity of the neurons to shifts in the audio frequency, just as, for example, in the visual system, well studied in this respect, the spatial summation takes part in creating the specific sensitivity of the neurons to the movement of visual stimuli.

At the same time it must be noted that for the appearance of responses to a shift in the audio frequency, it by no means has to take place in a short time. As was shown above (see Fig. 55), responses to changes in audio frequency are retained and have considerable amplitude even when the duration of the front of the stimulus (the time in which the change in frequency takes place) increases to tens of milliseconds, which made it possible to draw a conclusion as to the direct relation (within certain limits) of the amplitude of the evoked potentials occurring to the rate of change in the frequency. With a relatively slow change in the audio frequency, the excitation of the canals of the auditory system that discriminate the adjacent frequencies takes place not simultaneously, but sequentially, in the course of a given time interval, and the appearance of evoked potentials with this form of stimulus should be explained not simply as a spatial summation of the excitation, but as a certain dynamic feature of the temporal-spatial summation, which may be regarded as a specific mechanism of the reactions to a shift in the audio frequency.

Elements discriminating the shape of the spectrum of acoustic signals. The shape of the spectrum of the signal may be a feature of acoustic signals no less important than the nature of the change in the time of the basic frequency and amplitude. It does not appear possible to discuss all the characteristic changes in the spectrum of acoustic signals that may be of importance in analyzing these signals.

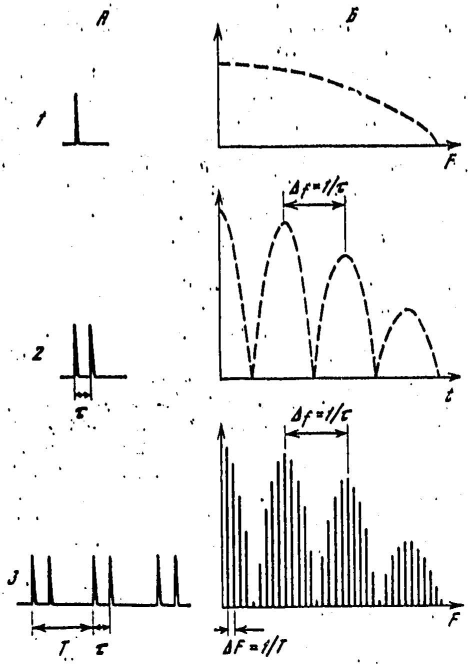


Figure 74. Spectrums of Signals Formed by Individual and Paired Pulses

A--shape of signal; B--spectrum of this signal; 1--individual pulse; 2--single pair of pulses; 3--continuous sequence of pairs of pulses. Other explanations in text.

We will discuss only certain characteristics of the spectrum of acoustic signals that are of interest in studying the dolphin's auditory system, and the possibilities of detecting specialized nerve elements that react to these spectral characteristics.

The suggestion was made (Dubrovskiy et al., 1970; Dubrovskiy and Krasnov, 1971) that there is great importance for dolphins' location identification of objects in the comblike shape of the spectrum, which may occur with the superimposing of two identical signals, shifted in relation to each other for a certain interval of time in the order of tens or hundreds of microseconds. The simplest method of forming signals with this spectrum is the transmission of paired identical acoustic pulses with short intervals between them.

The nature of the spectrums that signals formed by individual and paired pulses can have is schematically presented in Figure 74. If a click evoked by an individual pulse has a continuous spectrum of this type, as is shown in Figure 74, B, 1, then with the transmission of a pair of pulses with a brief interval t between them, the spectrum of the signal acquires a comb-like shape of a different type (Fig. 74, B, 2). In this case the peaks of the adjacent summits of the spectrum differ in intensity by a value of $\Delta f = 1/t$. This crested spectrum may occur not only in a click made by a single pair of pulses, but also in a continuous signal, for example, a noise, combined with its counterpart, delayed by the value t, or in a continuous sequence of pairs of pulses, as shown in Figure 74, 3. In the latter case the spectrum, just as all periodic signals, is in the nature of a line, but the spectrum envelope is described by a similar comblike shape with the distance between the crests $\Delta f=1/t$.

Special studies under free behavioral conditions (Vel'min, Titov, 1975) showed that dolphins easily distinguish pairs of such acoustic pulses if the interval between them lies within the limits of hundreds of microseconds (which corresponds to the distance between the crests of the spectrum of a signal from several kHz to tens of kHz) and is changed to tens of microseconds.

Of course, the dolphins' auditory system can hardly perceive separately two acoustic pulses with an interval in the order of 100 microseconds (the neural processes with the fastest response have a duration of a greater order). More probably, there is a perception of the two pulses in the pair as a single click, the spectral characteristics of which change depending on the interval between the pulses.

The question as to whether the dolphin's auditory system has specialized nerve elements which could identify the comblike shape of the spectrum is of unquestionable interest.

A very simple form of experiment aimed at solving this problem consists of comparing the evoked potentials of the cerebral cortex for individual acoustic pulses and for paired pulses with intervals in the order of tens to hundreds of microseconds.

Examples of the reactions to acoustic clicks evoked by an individual pulse and a pair of such pulses in an interval of 30 microseconds are shown in Figure 75, A and B. The shape of the evoked potentials and their amplitude with maximum forces of stimulus do not essentially differ. One can, however, note a substantial facilitation of responses to a click caused by a paired pulse, with low stimulus intensities: the paired pulse evokes a response of practically the same value as the individual pulse, the amplitude of which is tripled. In graphic form, the data of this experiment is more fully presented in Figure 76, which shows the relation of the amplitude of the evoked potentials of the cortex to the amplitude of individual and paired acoustic pulses with different intervals. It can be seen that for all the paired pulses the responses are considerably increased as compared with the responses to individual pulses of the same amplitude.

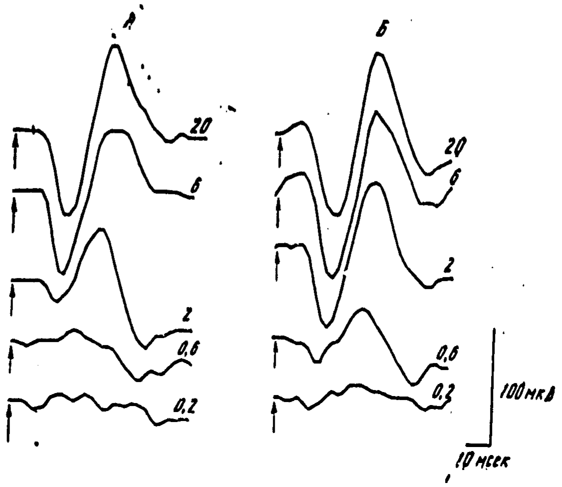


Figure 75. Evoked Potentials of the Auditory Cortex of the Brain of a Bottlenose Dolphin, Occurring in Response to a Click, Actuated by an Individual Pulse (Duration of the Pulse is 10 msec) (A) and a Pair of Similar Pulses With an Interval of 30 microseconds (B)

The intensity of the stimulus is indicated near the oscillograms as the level of the acoustic pressure of the click actuated by a single pulse, in n/m^2. The arrows denote the moments of stimuli.

It must, of course, be borne in mind that doubling the pulse with invariability of its amplitude does not in itself increase the power of the click generated, which should result in a corresponding shift in the force curves. When the pulse is doubled, however, the power of the click doubles, i.e., increases by 3 db. In the experiment performed, the effectiveness of the stimulus at the transition from the individual pulse to the paired pulse increases considerably more--by 10 db. It is hard to explain such a great increase in the effectiveness of the stimulus merely by the change in its power. One of the possible explanations of the results described may be the assumption that a change in the spectrum of the pulse (from uniform with an individual pulse to comblike with a paired pulse) made the stimulus more effective and capable of exciting the nerve elements of the cerebral cortex that were not excited or only slightly excited with the effect of the individual pulse.

Therefore, the results of the experiment are in accordance with the assumption of the existence of specialized nerve elements, sensitive to signals with a spectrum with a comblike shape, in the auditory system of dolphins.

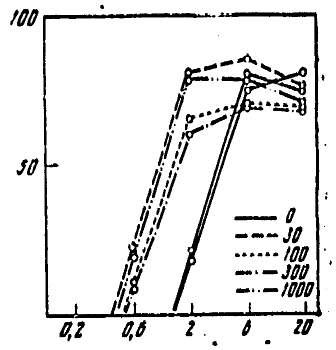


Figure 76. Relation of Responses of the Auditory Cortex to Clicks Actuated by Individual and Paired Pulses to the Intensity of the Stimuli

Along the axis of the abscissa--the acoustic pressure, measured by the peak value ofthe click evoked by an individual pulse, in n/m^2; along the axis of ordinates--the amplitude of the responses, in microvolts. At the right, near the appropriate symbols, the interval between the pulses in the pair, in msec, is indicated; 0--the individual pulse. The two graphs for the individual pulse were obtained from the results of measurements at the beginning and (for control) the end of the experiment.

Another proof that specific detector elements are present in a dolphin's auditory system that react to stimuli from a comb-shaped spectrum may lie in the experiments in which the evoked potentials of the cortex were induced directly by a change in the shape of the comblike spectrum. The experiments were conducted in the following manner. In the experimental tank a signal was sounded continuously, obtained by the actuation of a transmitter by a series of pairs of pulses, as shown in Figure 77, A. The spectrum of this signal consisted of lines, the distance between which was $\Delta F = 1/T$, where T is the repetition period of the pairs of clicks, and the spectrum envelope forms crests with the distance between them $\Delta f = 1/t$, where t is the interval between the clicks in the pair (see Fig. 74, 3). If $T \gg t$, then $\Delta f \gg \Delta F$, i.e., each crest of the spectrum is formed by a sufficiently large number of spectral lines. A change at a certain point in the time interval t between the pulses in the pair, with invariability of the parameters of each pulse and the repetition period of the pairs of pulses, served as the stimulus in the experiment described. This change in the shape of the signal corresponds to the change in the distance between the crests of the spectrum. The task of the experiment was to determine whether such a change in the spectrum of the acoustic signal could induce evoked potentials in the dolphin's cerebral cortex, and what parameters of the stimulus were necessary for this.

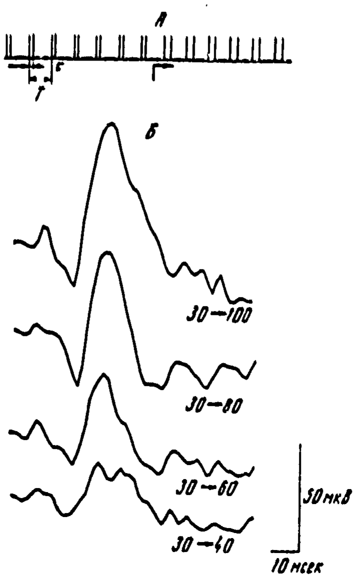


Figure 77. Evoked Potentials of the Auditory Cortex of the Brain of a Bottlenose Dolphin, Occurring in Response to Changes in the Intervals in the Pairs of Rhythmically Succeeding Acoustic Pulses

A--schematic representation of the shape of the stimulating signal. The repetition frequency of the pairs of clicks of 1 kHz (repetition period of the pairs, $T = 1000$ microseconds). The initial interval between the pulses in the pair is $t = 30$ msec. After the point marked by the arrow, the interval between the pulses in the pairs increases to 40-100 microseconds; B--evoked potentials occurring in response to this action. The beginning of the oscillograms corresponds to the moment of change in the intervals between the pulses in the pairs. The amount of change in the intervals, in microseconds, is indicated near the oscillograms.

It was discovered that at certain points of the cortex the stimulus through this method evoked distinct electrical reactions, occurring directly after the moment of the change in intervals between the pulses in pairs, i.e., in response to a change in the shape of the comblike spectrum of the sound signal. An example of these reactions is given in Figure 77 with various changes in the intervals between the pulses. The series of notations is shown in which the initial interval between the pulses was 30 microseconds (which corresponds to a distance between the crests of the spectrum of 33 kHz) and the stimulus was a change in this interval to 100, 80, 60 and 40 microseconds (distance between the crests of the spectrum respectively 10, 12.5, 17 and 25 kHz).

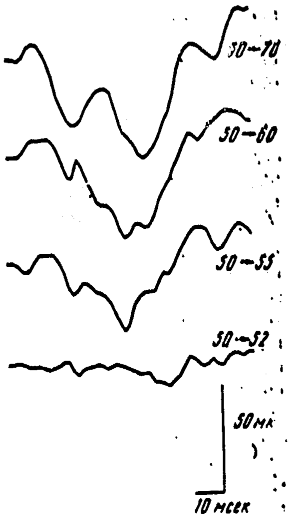


Figure 78. Primary and Slow Components of the Evoked Potential Occurring in the Auditory Cortex of a Bottlenose Dolphin's Brain in Response to a Change in the Intervals in Rhythmically Succeeding Pairs of Acoustic pulses

The amount of change in the intervals, in microseconds, is shown near the oscillograms.

It can be seen that the evoked potentials occurring in response to this action have a shape typical for the auditory cortex of a dolphin's brain, and are subject to the usual conformity to principle: they gradually reduce in proportion to the reduction in the values determining the physiological intensity of the stimulus--in this case this value is the change in the interval between the pulses. It is fully permissible to assume that the appearance of these evoked potentials was caused by the reaction of specialized nerve elements, reacting to the change in shape of the comblike spectrum of the signal.

In the reactions evoked by a change in interval between the paired pulses, there is also displayed the property described above of the responses of the dolphin's cerebral cortex as differing thresholds of fast and slow components of the evoked potential. As is shown in Figure 78, the change in the interval between the pulses may evoke a response containing both the initial component (peak 27 msec after the moment of stimulus) and the slow wave (peak 50-55 msec after the moment of stimulus). With a relatively large change in the interval between the pulses (from 50 to 70 microseconds), both components are clearly marked. With a weakening of the stimulus (change in the interval between the pulses from 50 to 60 and to 55 microseconds), first the early component weakens, and the slow wave appears more stable.

Elements discriminating a change in the intensity of the sound. As was shown above, a change in the intensity of a continuously sounding signal evokes in the dolphin's cerebral cortex a reaction in the form of evoked potentials. The question arises as to what type of mechanisms are involved in these reactions.

A very simple mechanism evoking the reactions to an increase or decrease in the intensity of the sound may be based on the existence in the cortex of neurons with different thresholds and with a more or less broad dynamic range of reactions for each neuron. With a heightening of the intensity of the sound it may become above the threshold for some of the neurons for which it was formerly subthreshold, which evokes a reaction of these neurons. In addition, the reaction of each neuron within certain limits depends on the intensity of the stimulus, and the increase in the intensity of the sound may evoke an increase in activation of these neurons. An increase in the number of activated neurons and increase in the level of excitation of the neurons should be reflected in the appearance of summary reactions of the nerve center being studied.

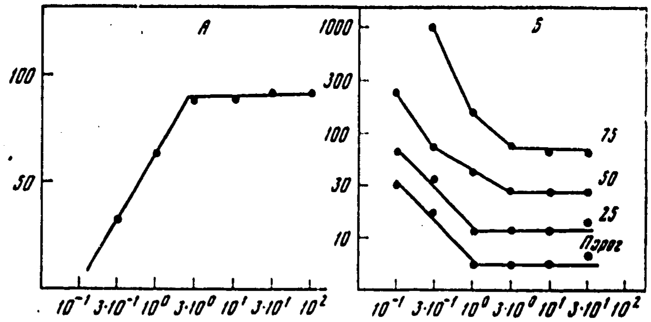


Figure 79. The Mechanism of Evoking Responses to a Change in the Intensity of the Sound

A--relation of the responses of the dolphin's cerebral cortex to starting a tone of 15 kHz to the intensity of the tone. Along the axis of the abscissa --the acoustic pressure, in n/m^2; along the axis of ordinates--the amplitude of the responses, in microvolts; B--the relation of the relative changes in intensity of the tone necessary for a response of a given amplitude to appear at the same point of the cortex to the initial intensity of the tone. Along the axis of the abscissa--the initial intensity of the tone, in n/m^2; along the axis of ordinates--relative change in the acoustic pressure, in % of the initial level. The amplitude of the responses, in microvolts, is shown near each graph. (a)--threshold

The experiments show, however, that the appearance of reactions to a change in the intensity of the sound cannot (at least in all cases) be explained in this way. This is evidenced by a comparison of the relation of the amplitude of the responses of the cortex to the intensity of the sound stimulus and thresholds of excitation of the responses to the change in intensity.

It was shown above that an increase in the amplitude of the evoked potentials with an intensification of the stimuli is observed only in a limited range of intensities, and with a further increase in the intensity, the amplitude of the responses that have achieved the maximum value no longer increases. It is obvious that this indicates that already practically all the elements were drawn into the reaction that had an activity that could be reflected in the summary evoked potential, and a further increase in the intensity of the sound could not increase either the number of elements drawn into the reaction or the reaction of each element. It could be expected that in the range of such high intensities, the reaction to small changes in intensity would be weakened in comparison with the reactions in the range of lower intensities.

The experiments, however, show a directly opposite conformity to principle. An example of such an experiment is given in Figure 79. At first the force characteristic of the cortical point being studied was plotted--the relation of the amplitude of the response to the starting of a tonal signal to the intensity of this signal. As can be seen in Figure 79, A, the reaction increases with an increase in the intensity of the sound from 0.1 to 3 n/m^2, i.e., in a range of about 30 db. With an increase in the intensity of the sound above 3 n/m^2, the amplitude of the response does not increase further.

Then, for the same point of the cortex, the relation was determined of the responses occurring to a change in the intensity of the tone to the initial intensity of the tone. The data was presented in the form of curves showing with which initial intensity of the tone and which relative change in the intensity a response of the given amplitude occurs (75, 50, 25 microvolts and the threshold response). It can be seen (Figure 79, B), that the relative threshold changes in the intensity, just as the changes in intensity necessary for the appearance of responses of a given amplitude, remain constant with relatively high intensities of sound (from 1-3 n/m^2 and higher) and increase with a reduction in the initial intensity of the sound.

If one compares graphs A and B in Figure 79, it is revealed that the responses to a change in the intensity of the sound are most effectively and with the lowest thresholds actuated precisely in the range of initial intensities (from 3 n/m^2 and higher), where on graph A there is a plateau, i.e., in the range in which these reactions cannot be the result of an increase in the number of elements drawn into the reaction to the starting of the sound, or an increase in the reaction of the elements already drawn in.

It is obvious that the nerve elements that generate the responses to a change in the intensity of the sound are rapidly and thoroughly adaptable, and do not react to a long sounding tone even of high intensity, but a change in the intensity of the sound, even a relatively small one, is an effective stimulus for them. Such thoroughly adapting elements may be regarded as specifically discriminating changes in the intensity of the sound.

13. Electrical Reactions of the Inferior Colliculus and the Corpus Geniculatum Mediale to Acoustic Stimuli

Reaction of the inferior colliculus. The inferior colliculus is an important auditory center, which in mammals not only implements independent processing of information, but also serves as a switching station on the path of conducting the afferent pulsation from the primary auditory centers to the corpus geniculatum mediale and cerebral cortex. Therefore, a study of the reactions of the inferior colliculus is of separate importance, and is also interesting for a comparison with the reactions of the underlying auditory centers.

A detailed study of the evoked potentials occuring in the inferior colliculus of the dolphin in response to acoustic stimuli was undertaken on narcotized animals (Bullock, et al., 1968) and subsequently on unnarcotized animals (Bullock, Ridgway, 1972). These studies described the form of evoked potentials occurring in the dolphin's inferior colliculus, and it was shown that these reactions were represented by quite short-latent and rapid (duration in the order of 1 msec) oscillations. The response consisted of several oscillations with latent periods from 2 to 4 msec; the specific form of the response, determined by the ratio of the amplitude of several oscillations included in it, depended on the point of contact.

Our studies show that the evoked potentials generated by the inferior colliculus of the dolphin's brain are characterized by a very expansive propagation of the electric field occurring during this, due to which the reactions of the inferior colliculus may be easily recorded, not only with the direct introduction of recording electrodes into this structure, but also at a certain distance in other structures of the brain.

It was shown above (Chapter 3) that in the dolphin's cerebral hemispheres, in response to an acoustic click, a rapid response (with a latent period of less than 2 msec and with a duration of a similar order) may be recorded. In this chapter the nature of this response was not discussed, and it was simply stated that it is not a response of the cerebral cortex, but is generated by other structures. A more detailed form of this response, recorded in the brain of a bottlenose dolphin, is shown in figures 80 and 81.

The latent period and temporal characteristics of the response, as can be seen from the oscillograms shown, coincides well with those described for the inferior colliculi of the dolphin's brain (Bullock, et al., 1968).
In consideration of the fact that in addition to the cerebral cortex, the

inferior colliculus is the auditory center with the most clearly developed "screening" structure, ensuring the best conditions for the generation of extended electric fields, it may be concluded that the inferior colliculus is the only structure that can be considered responsible for the generation of the evoked potential shown.

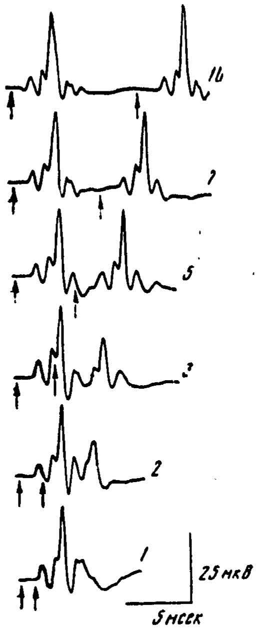


Figure 80. Responses of the Inferior Colliculus of the Brain of a Bottlenose Dolphin to Paired Acoustic Clicks

The arrows under the oscillograms note the moments of presentation of the clicks, and the intervals between them are represented in msec

The evoked potential of the inferior colliculus is a multi-component reaction: in figures 80 and 81, in the responses to the individual stimuli, oscillations are singled out with negative peaks for 2.1, 3, 4 and 6 msec after the stimulus, and with positive peaks after 2.6, 3.4 and 4.9 msec, as well as the later oscillations (latent periods are indicated without allowing for the time of conducting the sound from the hydrophone to the animal's head, which was about 0.5 msec). All the basic components of the evoked potential have a duration in the order of 1 msec and less, which is characteristic for the pulsed discharges of the nerve cells. It may be assumed that the summary evoked potential recorded reflects the synchronous occurrence of pulsed discharges in numerous presynaptic and (or) postsynaptic fibers (input and output) of the nerve elements of the inferior colliculus.

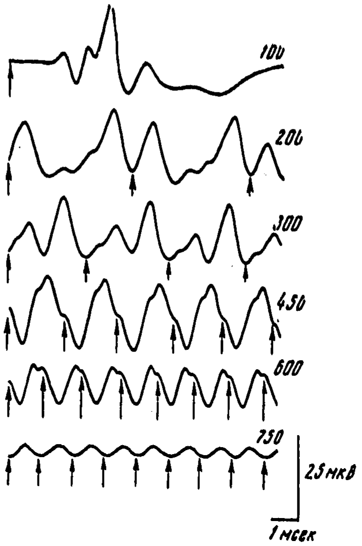


Figure 81. Responses of the Inferior Colliculus of a Bottlenose Dolphin's Brain to Rhythmic Acoustic Clicks

The arrows under the oscillograms denote the moments of stimuli, and the frequency of the clicks is indicated in pulses/sec

All the basic components of the response of the inferior colliculus display high resistance to repeated (paired and rhythmic) stimuli with short intervals. This property was noted earlier in a work (Bullock, et al., 1968), in which it was shown that with intervals between the acoustic clicks of 3-5 msec, the response to the second click is usually hardly depressed--it has an amplitude that differs little from the amplitude of the response to an individual click. In some cases the authors observed almost a complete regeneration of the response to the second stimulus with intervals of about 1 msec, and a partial regeneration--with intervals of about 0.5 msec. Accordingly, the succession of responses following a rhythm of acoustic clicks may be observed up to a frequency of 2000 pulses/sec. No easing of the responses to the second stimulus was observed at any intervals.

The recordings obtained by us of the responses of the inferior colliculus to paired and rhythmic acoustic clicks generally confirm these data. The reactions of the inferior colliculus to paired acoustic clicks are shown in Figure 80. It can be seen that the response to a repeated stimulus does not essentially differ from the response to the first stimulus, if the interval between the stimuli is 5 msec or more. A noticeable depression of the response to the repeated stimulus is observed only when the interval is reduced to 2-3 msec. With an interval in the order of 1 msec, a considerable depression of the responses at these short intervals may obviously be explained not as the effect of special inhibitory processes (since the synaptic processes usually have a duration measured in tens or hundreds of milliseconds), but by the refractory quality in the conducting paths along which the pulsed potentials of the action are propagated.

The ability of the responses of the inferior colliculus to appear at short intervals between stimuli is also well displayed if rhythmic acoustic signals are used. Examples of the reactions to clicks of varying frequency are presented in Figure 81. The responses may occur with quite high frequencies of the stimuli. When the frequency of the stimuli is 100 pulses/sec, the responses still differ little from the responses to individual stimuli. A change in the shape of the responses is observed only with the presentation of stimuli with a frequency in the order of several hundreds of pulses a second (in Fig. 81, from 200 to 450 pulses/sec), even though the amplitude of the responses remains high even at these frequencies. A considerable drop in the amplitude of the responses is observed only with an increase in the frequency of the clicks to 500 pulses/sec and over, although the responses of low amplitude may still be recorded with frequencies up to 100 pulses/sec (in Fig. 81, 750 pulses/sec).

An interesting phenomenon observed in rhythmic acoustic stimuli consists of a change in the ratio between the different components of the responses, depending on the frequency of presenting the stimuli. In Figure 81 it can be seen that with less frequent stimuli (100 pulses/sec), the main component of the response is a negative oscillation with the peak 4 msec after the stimulus, and the negative oscillation following it with a peak in 6 msec has a low value. With a stimulus frequency of 200 pulses/sec, however, these oscillations are almost comparable in value, since the first of them is somewhat reduced, and the second is increased. With a stimulus frequency of 300 pulses/sec, the second oscillation already dominates (with a negative peak 6 msec after the stimulus), and the earlier oscillation (its negative peak was shifted to 4.3 msec) is considerably weakened.

With higher stimulus frequencies, it is difficult to trace the contribution of individual components to the formation of a summation reaction, due to the inevitable smoothing out of the curve. Even the changes that can be traced with certainty, however, show that the ratio between different components of the reaction change substantially depending on the frequency with which the stimuli are presented. This phenomenon may be the result of the different quantitative characteristics of the refractory quality, the time summation and other processes taking place in different groups of the nerve elements generating the corresponding elements of the response of the inferior colliculus.

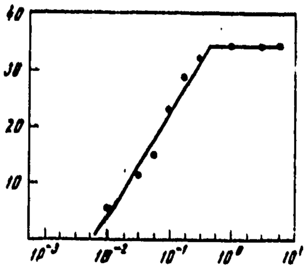


Figure 82. Relation of the Amplitude of the Responses of the Inferior Colliculus of a Dolphin's Brain to the Intensity of the Acoustic Clicks

Along the axis of the abscissa--the intensity of the stimulus (0.71 of the peak level of the acoustic pressure), in n/m^2; along the axis of ordinates--the amplitude of the responses, in microvolts

On the other hand, it is important to note the fact that at high frequencies of the stimulus, both the early and the later components are retained. If we assume that the recorded response of the inferior colliculus has both pre- and postsynaptic components, the later components of the response are more apt to be postsynaptic. Therefore, the retention of the later components at high frequencies of the stimulus may indicate that at such high frequencies not only pre-, but also postsynaptic responses of the inferior colliculus occur. In other words, this means that the inferior colliculus of the dolphin's brain may transmit the volleys of pulses with a high repetition frequency--up to hundreds of volleys a second.

From the responses of the inferior colliculus recorded it is possible to measure a number of the transmission characteristics of this auditory center, particularly--the force characteristic and threshold of excitation of the response. An example of a force curve obtained from measurements of the amplitude of the responses of the inferior colliculus with various intensities of the acoustic stimuli (clicks) is given in Figure 82. Just as in the cortical responses, the force curve of the responses of the inferior colliculus is divided into two parts: at high intensities of the stimulus (over 0.3 n/m^2), the amplitude of the response reaches the maximum value and does not depend on the intensity. With lower intensities, the amplitude of the responses depends approximately linearly on the logarithm of the intensity of the stimulus; this range occupies about 40 db. The threshold of excitation of responses, according to the results of this experiment, is estimated as a value of about $5 \cdot 10^{-3}$ n/m^2, which is close to the thresholds of excitation of the evoked potentials at a number of points of the dolphin's cerebral cortex.

A study was made (Bullock, et al., 1968) of the relation of the sensitivity of the responses of the inferior colliculus of the dolphin's brain to the frequency of the acoustic vibrations when brief transmissions of a pure tone are used as the stimuli evoking the responses. The relation obtained was different with different points of contact of the evoked potentials, which may be the reflection of a certain gonio-tonic projection in the inferior colliculus. The same thing is also indicated by the possibility of a substantial change in the form of the evoked potential (due to a change in the ratio between its individual components) with a change in the frequency of the stimulating tone. When combining all the data obtained from various points of contact, however, the summated relation of the thresholds of excitation of responses of the inferior colliculus to the frequency of the sound proved to be quite similar to an audiogram obtained for dolphins by using behavioral methods (sensitivity is maximal at a frequency of about 60 kHz and close to maximal in a range of frequencies of 20-70 kHz).

Also important are facts attesting to the presence in dolphins' inferior colliculus of specialized nerve elements that react discriminatorily to a change in the frequency of the sound (Bullock, et al., 1968). Namely, it was discovered that when frequency-modulated pulses are used as the stimuli (during the pulse, lasting 2-5 msec, a change takes place in the frequency of the duty cycle), responses may occur that are of much greater magnitude than when pulses similar in intensity and duration, but with a constant duty cycle frequency, are used. The effectiveness of the pulse with frequency modulation may depend on the direction of the modulation. The characteristics of frequency-modulated pulses could affect not only the overall amplitude of the evoked potential, but also its form, i.e., the ratio of its individual components. All these facts may be most rationally explained if one assumes that the individual components of the response of the inferior colliculus reflect the activity of specialized neurons reacting to a change in the frequency of the sound in a certain direction.

Reactions of the corpus geniculatum mediale. The corpus geniculatum mediale is the last switching station on the path of transmitting acoustic information to the cerebral cortex. Therefore, a study of the transmission of information through this center is very important for an understanding of the work of the entire upper thalamocortical level of the acoustic analyzer. So far there are no systematic studies of the reactions of the corpus geniculatum mediale of dolphin brains to acoustic stimuli. Individual observations of the reactions of this formation to acoustic stimuli, however, have occurred in our experiments, and the results of these observations may give preliminary ideas on the characteristic reactions of this auditory center of the brain.

The reactions recorded by us (evoked potentials) of the corpus geniculatum mediale to acoustic stimuli (clicks) had a relatively short latent period--5-6 msec. The complex of evoked potentials contained two basic components:

a rapid, two-phase oscillation with the duration of each phase 3-5 msec (time from the moment of stimulus to the peak of the first phase--9 msec), and a slower oscillation, with the time to the peak--23-25 msec (Fig. 83).

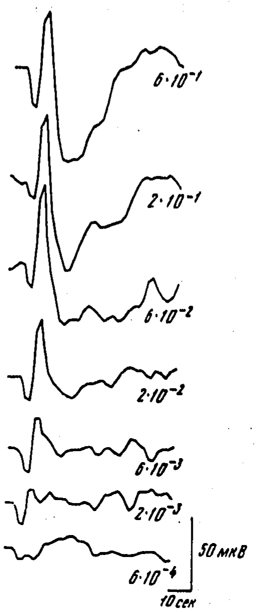


Figure 83. Evoked Potentials of the Corpus Geniculatum Mediale of the Brain of a Bottlenose Dolphin in Response to Acoustic Clicks of Varying Intensity

The intensity of the stimuli (0.71 of the peak level of the acoustic pressure) is indicated near the oscillograms, in n/m^2

These two components of the evoked potential have different properties, including different force characteristics. As can be seen from Figure 83, the slower component is well revealed only with relatively high intensities of the stimulus: 0.2-0.6 n/m^2. The fast component of the evoked potential, however, at this intensity is only negligibly reduced as compared with the responses to more powerful stimuli, and is retained, gradually diminishing, with the weakening of the stimulus below $2 \cdot 10^{-3}$ n/m^2. The force characteristics of the two components of the evoked potential constructed according to the data of this experiment are a good demonstration of the difference between them (Fig. 84).

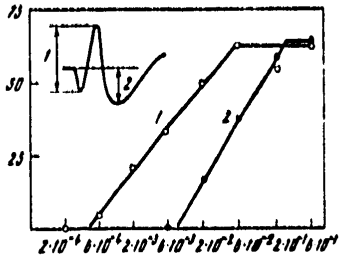


Figure 84. Relation of the Two Components of the Response of the Corpus Geniculatum Mediale of a Dolphin's Brain to the Intensity of Acoustic Stimulus (Click)

Along the axis of the abscissa--the intensity of the stimulus (0.71 of the peak level of the acoustic pressure), in n/m^2; along the axis of ordinates--the amplitude of the components of the response, in microvolts; 1, 2--fast and slow components of the response. The measurement of the amplitude of the components of the response is shown in the diagram

Another difference between the fast and slow components of the response of the corpus geniculatum mediale consists of the rate of their regeneration with paired acoustic stimuli. The fast component of the evoked potential is characterized by quite rapid regeneration. It has a substantial magnitude (over 50% of the normal) at intervals between the conditioning and testing stimuli of 10-15 msec (Fig. 85). The slow component requires longer intervals for regeneration: it appears at intervals of 20-25 msec and its amplitude is still noticeably reduced as compared with the norm at intervals of 100 msec and over.

A comparison of the different levels of the dolphin's auditory system (inferior colliculus, corpus geniculatum mediale, auditory cortex) with respect to the rate of regeneration of their responses during repeated stimuli is interesting. It was shown above that the responses of the inferior colliculus differ in their capacity for rapid regeneration with very short intervals between the stimuli--in the order of a few milliseconds. The responses of the cortex require considerably greater intervals between the conditioning and testing stimuli--over 100 msec--for complete regeneration. The responses of the corpus geniculatum mediale however (fast component of the evoked potential) with respect to the rate of regeneration, occupy an intermediate position between the responses of the inferior colliculus and the auditory cortex. This is clearly shown, if the mean characteristics of regeneration of the responses of these three structures with repeated stimuli are shown on a single graph (Fig. 86).

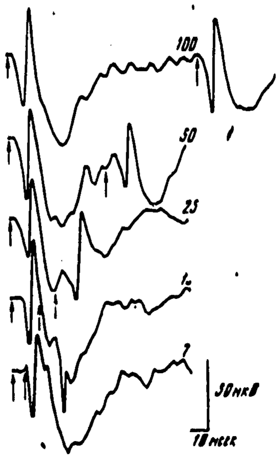


Figure 85. Responses of the Corpus Geniculatum Mediale of the Brain of a Bottlenose Dolphin to Paired Acoustic Stimuli (Clicks)

The moments of stimuli are marked under the oscillograms by arrows, and the intervals between the stimuli are indicated in msec

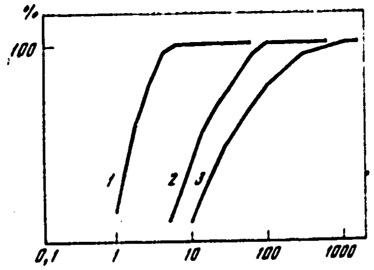


Figure 86. Comparison of the Regeneration Cycles of Evoked Potentials of the Inferior Colliculus, Corpus Geniculatum Mediale and Cerebral Cortex of a Dolphin

Along the axis of the abscissa--the interval between paired acoustic stimuli, in msec; along the axis of ordinates--the amplitude of the response to repeated stimulus, in % of the amplitude of the response to an individual stimulus; 1--inferior colliculus; 2--corpus geniculatum mediale; 3--auditory cortex

The properties of the responses of different levels of the auditory system may be a direct reflection of the interrelations between these nerve centers in the process of sensory analysis. The depression of the responses to repeated stimuli usually reflects the intervention of inhibitory processes which are caused by the conditioning stimulus and weaken the response to the testing stimulus. These inhibitory processes are the manifestation under specific conditions of the complex inhibitory interrelations between the neurons necessary for an analysis of the sensory information. At each succeeding level of the analyzer, additional inhibiting processes are drawn into the analysis of the information, which is manifested particularly, in a deeper depression of the responses to repeated stimuli in the upper levels of the system, as compared with the underlying ones. It may be considered that the losses of fast-response of the analyzing system (capacity to react separately to stimuli repeated after brief intervals of time) is the result of an increasing complexity of the operations performed, in proportion to the transmission of information from the periphery to the central divisions of the analyzer.

Summary

It is possible to study the procedures of information processing in the dolphin's auditory system both through recording the activity of individual neurons and through recording the summated electrical reactions. The method of recording the activity of individual neurons in a study of the dolphin's auditory system yielded a number of preliminary data, but the use of this method when working with dolphins is so far limited due to the difficulty of access to the material. The main results were obtained in studying the summated electrical reactions (evoked potentials) of the cerebral cortex.

A study of the relation of the amplitude of the evoked potentials of the cortex to the intensity of the stimuli is reflected by the force curves. The shape of the force curves may differ for different points of contact. The thresholds of excitation of reactions to starting a sound are about 10^{-3} n/m^2, which is close to the thresholds of absolute auditory sensitivity in dolphins. found by behavioral methods. Moreover, at a number of points of contact, the responses achieve the maximum magnitude when the intensity of the stimulus is only 15-20 db above the indicated threshold, which attests to the large number of low-threshold neurons in the dolphin's cerebral cortex. The responses to noise signals have lower thresholds than the responses to tonal signals.

The evoked potentials may occur not only in response to the starting or stopping of a sound, but also in response to a change (increase or decrease) in the intensity of the sound. The thresholds of excitation of these responses are 0.6-0.8 db, but with low initial intensities of the sound this value rises, so that the threshold changes in the acoustic pressure cannot be lower than the thresholds of the responses to the starting and stopping.

In studying the responses to sound transmissions of differing duration (from 1 to 20 msec), a time summation is discovered--an increase in the responses and lowering of their thresholds to 10-15 db when the transmissions are lengthened. At a number of points of the cortex, however, the opposite effect is also observed--a depression of the responses with an increase in the duration of the sound transmission.

Lengthening the front of the sound transmission results in a weakening of the evoked potentials. For certain points of the cortex a deep depression of the responses is already observed when the duration of the front is in the order of a few milliseconds, which cannot be explained only by the desynchronizing action of lengthening the front.

The evoked potentials in the cortex occur with a change in the frequency of a constantly sounding tone. The thresholds of excitation of these responses are 0.2-0.5% of the initial frequency.

The responses of the cortex to brief acoustic stimuli (clicks) are retained with paired and rhythmic stimuli with short intervals (up to 10 msec and less), even though they are considerably weakened. Accordingly, the responses to the rhythmic clicks may be reproduced by frequencies of stimulus up to 100/sec.

An investigation of the effects of masking is possible from the evoked potentials of the cortex. When a click is masked by a noise the responses to the click are depressed by 50%, when the effective levels of the acoustic pressure of the noise and the click are approximately equal; complete depression of the responses was observed when the noise was raised about 12 db above the signal. Tonal sounds only weakly mask the responses to the click: a rise in the noise above the signal of about 35 db is required to depress the response.

The relation of the responses to the tonal or noise nature of the signal, to the duration of the signal, change in frequency and other features may considerably differ at different points of the cortex. A number of points react well only to brief noise signals (clicks), with a steep front, i.e., signals of the type of locational pulses. Other points react well also to tonal signals of considerable duration and to changes in their frequency and intensity.

The study of the reactions of the cortex to stimulus with complex characteristics leads to the assumption that the dolphin's cerebral cortex contains neurons that react selectively to a number of features of the stimuli. The data indicate the existence of neurons that are sensitive to changes in the frequency of the sound (including a certain direction in the change of the frequency), intensity and specific spectral characteristics of signals with comblike spectrums.

Preliminary data were obtained on the properties of the responses of the inferior colliculus and corpus geniculatum mediale of the dolphin's brain. The responses of the inferior colliculus have a complex form and are of little duration (duration of the individual components in the order of 1 msec). They may reproduce the frequency of rhythmic clicks up to 1000/sec and over. The duration of the responses of the corpus geniculatum mediale and the capacity to reproduce the frequency of the rhythmic stimuli occupy an intermediate position as compared with these indicators for the inferior colliculus and the cortex.

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