QUESTIONS CONCERNING THE PHYSIOLOGY OF THE ORGAN OF 
HEARING AND THE LATERAL LINE OF FISHES

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Some questions on the physiology of the auditory organ and the lateral line of fishes.

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For a number of years, we have, under the direction of K. H. S. Koshtoyants, studied the physiological peculiarities of a specific analyzer or receptor which is adapted to the conditions of an existence in water, as the organ of the lateral line of fishes. The results of these studies were reported at the XVI Pavlov convention, part of them was published. For this reason I will pause very briefly only at the main results so that the experiments, which I will report today, will be understood.

The purpose of our studies was to establish which frequencies of vibrations of the aquatic medium are adequate for the analyzer or receptor of the lateral line of the fishes, i.e. what is the frequency-diapason of perception like. By means of the conditioned reflexes, together with the chronic exclusion of the organ of the lateral line and the auditory organ, we succeeded in showing that the organ of the lateral line of carassius receives vibrations from 1 to 25 hertz inclusive. In connection with this it was established that the auditory analyzer or receptor of these fishes receives vibrations from 18 hertz and more. Thus it was established that there exists for the receptor of the lateral line and the auditory receptor a common diapason of the
perceptible frequencies, i.e. vibrations with a frequency from 18 to 25 hertz are adequate for the analyzer or receptor of the lateral line as well as the auditory receptor of those fishes. Such a functional similarity of the organ of the lateral line and the auditory organ is in keeping with their common origin, the similarity of the construction of the terminal apparatus and "kinship" of the central nuclei of these two analyzers or receptors. There is a functional similarity also in the qualities of these receptors. This will be seen below.

When studying the organ of the lateral line as an analyzer or receptor it would be interesting to establish whether this organ is capable of discriminating between the vibrations perceived on the frequency and what is its analyzing capacity like. Experiments with the development of differentiations or discriminations have shown that the receptor of the lateral line of a carassius is capable to discriminate between vibrations on the frequency. A discrimination of frequencies of 3 hertz is the limit.

In order to make a more thorough study of the analyzer or receptor of the lateral line we undertook research work to locate the central link of this receptor. By combination experiments of the various sections of the brain with the development of conditioned reflexes we succeeded in showing that the leading part of the brain in bringing about the conditioned reflexes from the organ of the lateral line cerebrum or brain. Such is a brief summary of the research carried out. This research
made it possible to carry on this work which was to established whether to a fish by means of receptor of the lateral line of determining the direction of the vibrations perceived.

Several authors who studied the organ of the lateral line of fishes pointed out the probable capacity of fish to localize the place of the source of the vibrations of low frequencies. However special research has not been carried out so far. Nevertheless, this question plays an important role in the characteristic of a receptor such as the organ of the lateral line which is showed important for the conditions of an existence in water.

Our experiments as well as the former experiments were conducted by means of the conditioned reflexes method. The motive food methods of the maybe recording developed by N. V. Prazdnikova (1953) in the laboratory of L. G. Voronin were applied. The experiments were conducted with carassius and carp. The conditioning excitant or stimulus were vibrations of the aquatic medium of a low frequency. The extra food of fish with moths was used as an unconditioning excitant or stimulant. The conditioned reaction was express by the fact that in response to the switching on of the vibrator the fish swam to the feeding place. In other approaching this place closed a special device which was connected with the electric circuit. This was recorded on the kymogram. The experiment was carried out as follows. In one corner of the aquarium (drawing 1) there was placed a vibrator concealed from the fish and on it there was developed a positive conditioned reflex. After this as this reflex was fixed by a number of experiments a negative vibrator, i.e. such action was
never strengthen was placed in the opposite corner of the aquarium. Both vibrators performed on the same frequency and amplitude. They differed only by their location.

After a lengthy stage of generalization when the fish reacted positively to the positive as well as the negative excitant or stimulus there appear the differentiation or discrimination. At the time of the 67th—to the 86 trial or application of the negative vibrator it had become fixed and the fish now clearly discriminated. Thus it was shown that by means of the receptor is lateral line of the fish, the fish able to tell the direction of the vibrations perceived by it.

The results obtained by us confirmed the observations by N. N. Diaslar (1941, 1948, 1953) A. P. Andreyashev (1944, 1944a,b), Digkgeaf 1934 and of other researchers who spoke of the organ and the lateral line to recognize vibrations of a latter frequency.

As they pointed out our experiments disclose that the organ of the lateral line of the auditory organs of fish are similar as regards to the structure and origin have a common diapason of the frequencies perceived. This indicates their functional similarity. If the organ of the lateral line is capable to tell the direction of the vibrations perceived then, naturally, a question is facing us; is the organ, which is genetically close to it near the auditory receptor also capable of determining the direction of sound? This question has intensified the ichthyologists and physiologists for a long time, but it has not been studied thoroughly. The early researchers when observing
the ability of fish were inclined to solve this problem in a positive sense. However, Reinhard (1935) as well as Frisch and Digkgraaf (1935) who trained sheat fish and minnows to respond to sound came to the conclusion that the fish are incapable of telling the direction of the sound. From then on it was the consensus of opinion that the fish cannot determine the direction of a sound. After this is corrected it becomes incomprehensible how in a biological sense such adaption as the emitting of sounds by a number of species of fish it is known that of such there are about 100 species picked appearance of a “voice” in the males of certain fish during the spawning period can be justified. For the other individual would not be able to tell from which direction the sound came.

The general considerations as well as for the nature for the experiments of Frisch Digkgraaf and Reinhard were carried out with methodical errors and compelled us to cast doubt upon the date by the enumerated authors and to conduct experiments which would help to clarify this question. In the experiments conducted with carp we also used the motive food methods. The sound was created by a sound-generator and was "piped" into the aquarium by means of an emitter which was hidden from the fish and was placed in such a way as not to create lateral vibrations. The frequencies sound was applied on the frequency of 200 hertz.

The first series of experiments was set up in the same way as the experiments with vibrations of a low frequency (drawing 1a), i.e. a conditioned reflex to sound in a certain place in the
aquarium was developed. After this as the reflex was fixed during a number of experiments in another place in the aquarium the same sound was produce (which differed from the first only by the direction), but without the food reward. After a lengthy stage of generalization the fish began to tell the sounds apart. About the 75-96 trial application of the negative conditioning excitant or stimulus the fish was able to differentiate clearly between the two sounds. Thus the experiments of this series showed that the auditory analyzer or receptor of fish is capable of telling the direction of the sound.

We came to the same conclusion in another series of experiments which was conducted in the following way.

In one corner place of the aquarium a sound-emitter which was shielded or hidden from the fish was placed. (drawing). They approached to the place of the sound they rewarded with food. A conditioned reflex to this sound was developed. When the reflex became fixed we began to develop a reflex to the same sound but which was placed in the opposite side of the aquarium. After this as the reaction to this sound became stable we combined both sounds in the experiments and alternated them without adhering to a definite order. At first we observed a generalization of both signals. It required more than 100 trials or applications of stimulus until the specialization became, i.e. the given stimulus was sounded the fish approached it and not the other.

Thus both series of experiment showed that the auditory receptor of carp is capable of determining the direction of the
sound perceived. Our data agreed well with the results obtained by Kleerekoper and Chagnon (1954) who in a different experiment than ours obtained data that indicated that fish can tell the direction of sound. However it seems to us that we must be sure that the results obtained by the above mentioned authors and by us any aquaria are applicable also to natural conditions. Therefore, it is necessary to check this result by experiments in opened water.

Frisch and Digkraaf who denied the ability of the fish to determine the direction of sound explained this by the fact that the auditory organs of a considerable number of species of fish are connected with an odd or unpaired organ, namely, the swim bladder which most likely brings about simultaneous "hearing". In their opinion the sound is perceived by the wall of the swim bladder. These vibrations are transmitted to both weberian apparatus end through them simultaneously into the labyrinths. It is known that the direction of a sound is determined by a difference in the time of the arrival of the same phases in both ears or by the difference of the intensities of the sound in the ears. Such a notion excludes both moments mentioned seeing that sound reaches both simultaneously with an equal intensity thus makes it impossible to determine the direction from which the sound came.

Drawing 2. Connection of the labyrinths with the swim bladder in cyprinoid fish (from Frisah).

1- Utriculus; 2- Sacculus; 3- Lagena; 4- Sinus imper; 5- the Weberian ossicles; 6- Swim bladder; e-a1- place of the cut.
The data obtained by us are incompatible with such a notion of the perception of sound. Therefore we decided to check experimentally whether there actually exists a similar mechanism for the reception of perception of sound. In order to solve the assigned problem it became necessary, by a chronic operation to sever the connection between the inner ear and the swim bladder. This was done at the place of the junction of the Weberian apparatus with the air bladder (drawing 2).

In order to be absolutely sure that there was no contact between the swim bladder and the Weberian apparatus we removed the entire anterior chamber of the swim bladder. In the case of carassius the operation impaired the capacity to swim. This induced us to forego the use of the motive-food methods and to switch to the electric-defensive methods. The conditioning excitant or stimulus, as before, was sound. The non-conditioning stimulus was the effect of a weak electric field. The current supplied to the electrodes, submerged in water, was applied from a stimulator which made it possible to produce impulses of the required form, frequency and duration and smoothly change or alter the tension.

The results of the experiments with carassius showed that the conditioned reflexes to sound had been retained and could be developed anew in the fishes in which the connection between the inner ear and the air bladder had been severed.

Another series of experiments was conducted in connection with the fact, as discovered in mirror carp (in distinction from
carassius) that the removal of the anterior chamber of the entire air bladder did not at all affect their ability to swim. This made it possible to conduct experiments according to the motive food methods. In these experiments as well as in the experiments with carassius the conditioned reflexes to sound were retained and could be developed anew.

Thus the results of two series of experiments showed that and the inner ears is when the connection between the swim bladder severed and even when the entire swim bladder is removed the fish does not lose its sense of hearing. Therefore the view that the swim bladder plays a part in the receiving apparatus, so it seems, must be regarded as erroneous. And if that is so then the main argument of the researchers, who deny the capacity or ability of fishes to determine or to tell the direction of a sound, collapses.

The experimental data obtained can be summarized as follows.

Experiments for developing discriminations to vibrations of a low frequency showed that by means of the analyzer or receptor of the lateral line fish can localize the source of sound.

Experiments with discrimination as well as with distinguishing between two sounds on the basis of the directions only showed that the auditory receptor of cyprinoid fish can tell or determine the direction of a sound.

The disruption of the connection between the inner ear and the swim bladder does not cause the loss of hearing in fish.

Drawing 1 (page 33)

Chart of experiments with sound and low frequency vibrations.