

PHYSIOLOGY

THE REFLEX REGULATION OF THE ACTIVITY OF THE HEART IN FISHES

COMMUNICATION I. REFLEX ACTION ON THE HEART FROM STIMULATION OF THE AFFERENT FIBERS OF THE MESENTERY AND INTESTINE

I. M. Rodinov

Department of Physiology of Animals (Head – Corresponding Member AN SSSR,
Active Member AN Armenian SSR Prof. Kh. S. Koshtoyants) of the Faculty of
Soil Biology of Moscow State University

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Fishes represent an object of exclusive interest for the study of the regulatory action of the vagus nerve on the heart. No similar object can be found among any other class of vertebrates, since the vagus nerve is the only pathway of effector innervation of the heart in fishes. Some authors consider that the sympathetic system in fishes is generally not connected to the heart [6-10]. We can at least take it for granted that this innervation has no essential regulatory importance. Particularly convincing in this respect are the findings of V. A. Shidlovskii [5], who stimulated the cranial part of the sympathetic chain and observed merely an increase in the amplitude of the contractions of the sinus venosus without any accompanying change in the rhythm and working of the remaining divisions of the heart. Bearing in mind that the leading division of the heart of the teleost fishes is situated not in the sinus but in the auricular canal of the atrium, these findings may be regarded as proof of the absence of any form of active sympathetic innervation of the heart in fishes.

On the basis of findings demonstrating the presence of only one pathway of effector innervation of the heart in fishes, Skramlik [9] evolved a theory of nervous regulation of the cardiac activity of these animals. According to this theory, the high "intrinsic automation" of the fishes' heart is under the constant inhibiting tonic action of the vagus nerves. From this point of view, bilateral regulation of the rhythm of the heart is effected by means of changes in the intensity of the tonus. A quickening of the cardiac rhythm is the result of weakening of the specifically inhibitory influence of the vagus nerve. Direct experimental examination of Skramlik's theory does not confirm it. According to the experimental findings of B. S. Kulaev [1], division of the cardiac branches of the vagus nerves or isolation of the heart of a fish does not produce a quickening of its rhythm in the majority of experiments. Isolated cases of transient, brief quickening of the rhythm after division cannot be regarded as the result of abolition of the inhibitory tonus of the vagus nerves.

A point of view of the regulatory role of the vagus nerves which differs in principle is that developed by M. G. Udel'nov and his co-workers [1-4]. These workers showed that the vagus nerve may bring about bilateral regulation of the action of the heart as a result of an active discharge of impulses. The development of an inhibitory or stimulatory effect is determined by the quantitative characteristics of the homogeneous effector impulses passing along the vagus nerve. These conclusions are based on findings obtained on a series of vertebrates, including fishes [1, 2]. It becomes necessary to discover in what way it is possible for the vagus nerve to act as universal regulator of the activity of the heart when the activity of the animal is reflex in nature. There are many findings which show that in this case the quantitative characteristics of stimulation of the efferent fibers play a very important role in determining the nature of the reflex response [1, 3].

We set out to study the possibility of obtaining, by means of reflexes, dual effects — inhibitory and stimulatory — on the heart of fishes, and of determining the characteristics of the afferent stimulation required to produce either effect. We performed parallel experiments in order to test the conclusion of previous authors on the absence of inhibitory tonus of the vagus nerves.

EXPERIMENTAL METHOD

Experiments were carried out on different species of teleost fishes — pike, perch, roach, bream, burbot, crucian and sheat-fish. Forty acute experiments were performed. The fish were fixed on a board with its ventral region uppermost. The abdominal wall was opened by a transverse incision slightly below the bones of the shoulder girdle. Through a longitudinal incision along the midline, directed toward the head, the bones of the shoulder girdle were divided and partially removed. The heart, situated beneath them, was freed from the pericardium. The cardiac contractions were recorded by means of an Engelmann's lever. In order to stimulate the mechanoreceptors of the intestine (Goltz's reflex), the peritoneal cavity was opened and the intestine extracted. The mechanoreceptors were stimulated by tugging on a ligature applied 5-7 cm distal to the beginning of the small intestine. In order to stimulate the individual nerve branches, the intestine was extracted from the peritoneal cavity, stretched out and fixed to a special frame. The individual nerve trunks in the mesentery were dissected out and their central ends were then stimulated by an induction coil. Experiments in which the individual branches leading from the intestine were stimulated were carried out only on those species of fishes in which the mesentery was sufficiently well developed — the sheat-fish and burbot.

EXPERIMENTAL RESULTS

Experiments to study the properties of the Goltz reflex in fishes were carried out on pike and perch. In the pike the Goltz reflex was expressed mainly in the form of inhibition of the cardiac activity; a quickening of the heart's action developed only in comparatively rare cases. In the perch, on the other hand, stimulation of the mechanoreceptors of the intestine caused as a rule a quickening of the cardiac activity, and only in isolated experiments was the rhythm slowed (Fig. 1). The vagus nerve is the only pathway of effector innervation of the heart in fishes, and it may therefore be thought that both inhibitory and stimulatory effects observed in our experiments were brought about by means of the vagus nerves. The experiments did in fact show that after bilateral division of the common vagus trunk in the branchial pouch, no reflex changes could be induced in the activity of the heart.

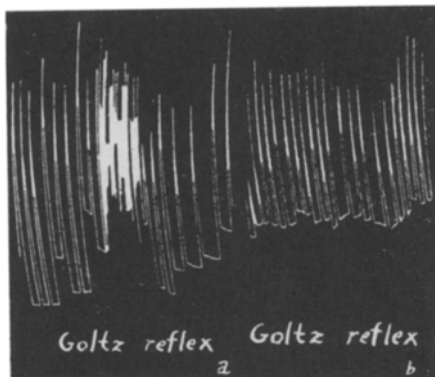


Fig. 1. Changes in the rhythm of the heart in fishes during stimulation of the mechanoreceptors of the intestine. a) Quickening of the heart beat in an experiment on the perch; b) inhibition of the heart beat in an experiment on the pike.

We carried out experiments to study the afferent pathways of the Goltz reflex in fishes. The centripetal fibers of the intestine and stomach subjected to mechanical stimulation may take two paths: first, in the structure of the vagus nerve, and secondly, in the structure of the splanchnic nerve. The former pass directly to the medulla oblongata; the latter first enter the spinal cord and then ascend to the superior division of the central nervous system. By dividing the spinal cord we could exclude the influences passing along the splanchnic nerve without disturbing the integrity of the reflex arc whose afferent and efferent parts were contained in the vagus nerve. The experiments showed that division of the spinal cord between vertebrae III and IV and between IV and V made it impossible to obtain reflex responses from the heart to stimulation of the intestine (Fig. 2). These findings showed that the afferent pathway of the reflex on the heart elicited by stimulation of the intestinal receptors take a course in the structure of the splanchnic nerve.

We were thus able to see that both stimulatory and inhibitory reflex effects on the heart could be obtained from the same receptive field. The necessity arose of ascertaining the distinctive features of afferent stimulation that could lead to the appearance of heterogeneous reflex responses. On the basis of the experimental findings of M. G. Udel'nov [3] and B. S. Kulaev [2], showing that the frequency and the strength of stimulation or the number

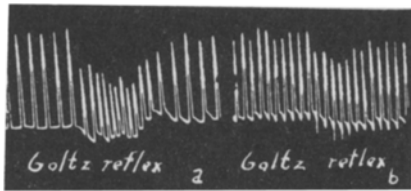


Fig. 2. Experiment on the pike. Disappearance of the reflex response of the heart to stimulation of the mechanoreceptors of the intestine after section of the spinal cord between vertebrae III and IV. a) Original reflex; b) after section the changes in the rhythm of the heart are absent.

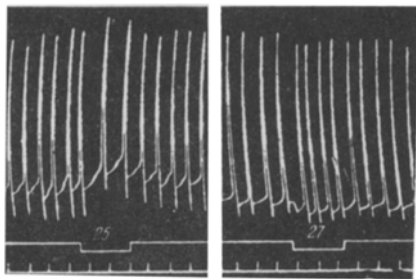


Fig. 3. Experiment on the sheat-fish. Stimulation of the same branch of the splanchnic nerve in the mesentery with different strengths (coil distance 25 and 27 cm) elicits opposite changes in the rhythm of the contractions of the heart. Significance of the curves (from above down): mechanogram of the heart, stimulus marker, time marker (5 sec).

response to reflex stimulation, and in this case, moreover, both may be obtained from the same receptor field. The factor which determines the character of the response in any given case is the strength of afferent stimulation.

of active afferent fibers may be the deciding factor of the eventual reflex response, we performed experiments to determine the role of the intensity of afferent stimulation in the production of heterogeneous reflex responses of the heart. It is difficult to regulate the degree of mechanical stretching of the intestine with accuracy, and we accordingly used electrical stimulation of the individual branches of the splanchnic nerve in the mesentery. In a series of experiments we succeeded in discovering a relationship between the strength of stimulation of these branches and the character of the reflex response: quickening appeared as the result of relatively weak stimuli, and in response to stronger stimuli inhibition of the activity of the heart was observed. The result of one of these experiments are given in Fig. 3.

The information given suggests that as a result of reflexes acting through the vagus nerves, the only pathway of effector innervation of the heart in fishes, both inhibitory and stimulatory effects may be obtained. It was thought to be very important to satisfy ourselves once again of the absence of an inhibitory tonus acting on the heart in fishes, and to confirm in this way the active character of the influences causing inhibition and quickening of the rhythm of the heart. For this purpose we carried out 13 experiments on different species of fish (pike, perch, roach, bream, crucian and sheat-fish) and studied the changes in the rhythm of the heart after complete isolation of the organ. These experiments fully confirmed the conclusions of the authors who had previously studied this question [1]. In only one experiment was quickening of the rhythm observed after isolation; in two cases there was a temporary quickening, transient in character, and in the remainder either no changes were generally observed or the rhythm became slower.

These results clearly indicate the absence of an inhibitory tonus affecting the heart in fishes. Both quickening and inhibition of cardiac activity are therefore the result of active influences passing along the vagus nerve to the cardiac muscle. This dual response of the heart is also observed in re-

SUMMARY

The author studied the reflex control of the fish heart which has only one path of effector innervation, viz., the vagus nerves. Literature and personal data show that inhibitory tone in the heart is absent in fish. In stimulating intestinal receptors there appears, depending upon the strength of the afferent stimulation, inhibition or acceleration of the cardiac activity.

Hence both effects may be considered as the result of an active impulse of the vagus nerve on the heart.

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