# THE REFLEX CONTROL OF THE CARDIAC ACTIVITY IN FISHES

## COMMUNICATION II. REFLEX EFFECTS ON THE HEART AND INTESTINAL VESSELS IN RESPONSE TO STIMULATION OF THE PRESSURE RECEPTORS OF THE BRANCHIAL VESSELS

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The heart of fishes, in contrast to that of other vertebrates, has only one pathway of effector innervation, the vagus nerve. The fish is therefore an object of peculiar interest in the study of the regulating effect of this nerve on the heart. There is evidence that no inhibitory vagotonic action on the heart is present in the fish [1, 3]. Any increase in the heart rate arising as the result of nervous action must, therefore, be regarded as the result of an active impulsive influence of the vagus nerve on the heart. It was shown in the previous communication [3] that both inhibitory and stimulatory effects could be obtained reflexly from the same receptive field (the receptors of the intestine), and moreover that the stimulatory effect is the result of weaker afferent stimulation than the inhibitory. These findings support the view [4, 5] that active impulses, passing along the vagus nerve, may exert different effects—inhibitory and stimulatory—on the action of the heart.

There is experimental evidence in the literature of the presence of receptors in the branchial vessels of the fish [9, 11, 12]. It has been shown [2] that in response to stimulation of the branchial nerves, depending on the number of fibers stimulated and on the strength of stimulation, both a slowing and a quickening of the rhythm of the cardiac action may develop.

This communication is devoted to further investigation of the controlling influences exerted on the heart of fishes, depending on the intensity of afferent stimulation.

Stimuli were applied to the pressure receptors situated in the abdominal aorta and the afferent branchial vessels. The choice of this particular reflexogenic zone was made not only on account of the relative ease of adequate stimulation and variation of the intensity of stimulation of the receptors situated therein, but also because the branchial vessels, so far as their sensory apparatus is concerned, are the homologs of such reflexogenic zones as the aorta and carotid sinus [6, 10].

## EXPERIMENTAL METHOD

Experiments were carried out on bony fishes — sheat-fish, carp and tench (35 experiments),— and also on two species of ray-fish — the long-tailed skate and sea-fox (12 experiments). Fixation of the fishes and recording of the cardiac contractions were carried out as described in the first communication [3]. In the dissection of the branchial vessels, the skin over the lower jaw was incised along the midline. The connective tissue film covering the abdominal aorta and the afferent branchial vessels was exposed and divided. A cannula was inserted into the peripheral end of the vessel. The corresponding efferent branchial vessel was ligated. The cannula was connected to a burette, filled with Ringer's solution, which was used to distend the vessel. The pressure was calculated in cm of water. After the conclusion of stimulation the pressure in the vessel was made equal to

atmospheric. In addition to the reflex effects on the heart from the branchial vessels, we also recorded the velocity of the blood flow through the intestinal vessels and the movements of the gill coverings.

In order to record the vascular effects an area of the small intestine of the fishes was perfused with Samoilov's solution. The nerve supply of the perfused area was left intact. The frequency of falling of drops of perfusing fluid flowing from the vein was recorded. All the experiments of this series were performed on sheat-fish.

## EXPERIMENTAL RESULTS

The experiments showed that during distension of the branchial vessels with varying force, both stimulatory and inhibitory changes could be produced reflexively in the action of the heart. The character of the response did not depend on which of the five branchial vessels was distended. Biphasic reflex responses could develop in the heart from any of them. Inhibition of the heart's rhythm arose, as a rule, in response to stronger stimulation than that producing an increase in the rate of the heart. Fig. 1 illustrates an experiment in which distension of the vessel with a pressure of 11 cm of water caused a sharp slowing of the rate of the heart, and with a pressure of 6 cm, a quickening of the rate.

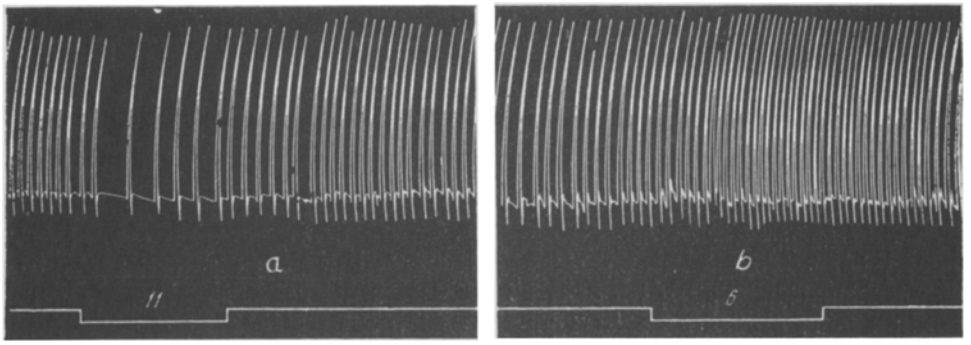


Fig. 1. Experiment on a long-tailed skate. Different forms of reflex change in the rhythm of contraction of the heart with increase in the pressure in the first branchial vessel to 11 cm (a) and to 6 cm (b) of water.

Weak stimulation evidently activates a smaller number of sensory endings than stronger. Discharge of impulses from each individual receptor is also, probably, more frequent in response to stronger than to weaker stimulation. In view of these considerations it may be thought that the reflex inhibition of the cardiac activity in response to stretching of the receptors of the branchial vessels arose as the result of a large number of impulses passing to the central nervous system, and that a smaller number caused the opposite effect, an increase in the rate of the heart.

We found this relationship described between the strength of distension of the branchial vessel and the character of the reflex response of the heart in several species of fishes, in the 2 species of ray-fish, carp, crucians and sheat-fish.

In Fig. 2 are shown the results of one of the experiments on the sheat-fish. Stretching with a force of 40 cm was accompanied by a slowing of the heart rate, whereas a smaller stretching force caused a sharp increase in the rate of contraction of the heart, giving place, very soon, to inhibition. This secondary effect was evidently due to overstretching of the remaining branchial vessels in consequence of the quickening of the heart's action.

Depending on the degree of afferent influences from the branchial vessels, both stimulatory and inhibitory effects may thus be reflexively produced on the heart. Bearing in mind the information given in the previous communication, it must be realized that both effects arose as a result of the effect of an active flow of impulses along the vagus nerve to the heart. The character of the response, i.e., stimulation or inhibition of the rhythmic action of the heart by reflex excitation, was dependent on the number of afferent impulses reaching the central nervous system in unit time.

It is easy to understand the adaptive importance of the relationship described between the pressure and the changes in the working of the heart. In fact, a low pressure in the vessel is a signal of inadequate filling of the abdominal aorta with blood, creating unsatisfactory blood supply conditions for the tissues. The adaptive response to this is an increase in the heart rate and a more intensive redistribution of blood from the venous to the arterial part of the blood stream. A high pressure in the vessels, i.e., overfilling of the branchial vessels with blood, on the other hand, causes inhibition of the cardiac activity and the temporary diminution or cessation of the entry of blood into those vessels.

The function of the pressure receptor zone of the branchial vessels of fishes differs in certain features from that of the homologous zones of the carotid sinus and aorta. If, when the abdominal aorta is well filled with blood, the conus arteriosus of the fish is divided, and the branchial vessels thereby completely emptied, no stable or considerable changes in the rate of the heart are induced. The pressure receptors of these vessels in fishes do not, therefore, exercise a constant control over the level of the blood pressure, as occurs in the warm-blooded animals [7, 8]. It is possible that the absence of tonic reflex influences from the branchial vessels of fishes during their prolonged distension is due to the rapid adaptation of the receptors of this reflexogenic zone to a constant pressure [9].

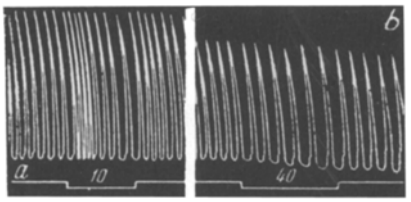


Fig. 2. Experiment on the sheat-fish. Reflex changes in the heart rate by increasing the pressure in the third branchial vessel to 10 (a) and to 40 (b) cm of water.

It appeared of great interest to determine the character of the reflex effects on the vessels in response to stimulation of the receptors of the reflexogenic zone under study. Experiments showed that during distension of the branchial vessels considerable changes could be observed in the volume of perfusate flowing through the intestinal vessels. The vasomotor reflexes were expressed both in the form of dilatation and constriction of the vessels. Fig. 3 illustrates the vasoconstrictive effect caused by an increase of pressure in the branchial vessel, accompanied by a slight slowing of the cardiac activity. Attempts to establish a relationship between the strength of distension of the vessel and the character of the vasomotor response gave less definite results than did the experiments on the heart, but in some cases it was possible to show that the pressor response arose at a lesser degree of distension than the depressor response. It was only comparatively rarely, however, that such a relationship could be observed in a clear form.

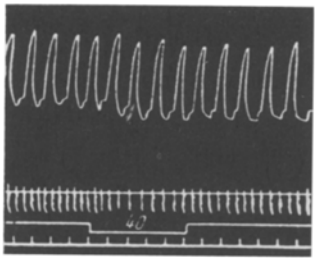


Fig. 3. Experiment on the sheat-fish. Reflex constriction of the intestinal vessels and inhibition of the rhythm of the heart by increasing the pressure in the first branchial vessel to 40 cm of water. Significance of the curves (from above down): mechanogram of the heart, recording of the fall of drops of perfusate flowing through the intestinal vessels, stimulation marker, time marker (5 seconds).

During simultaneous recording of the action of the heart and the vascular reactions it was not possible to show connections between a particular reflex effect on the heart and a particular vascular reaction. For example, inhibition of the rhythm of the heart could be accompanied by either constriction or dilatation of the intestinal vessels.

An increase of pressure in the branchial vessels also had a reflex influence on respiration (movement of the gill coverings). Under these circumstances the most varied changes could be observed: quickening or slowing and increase or decrease of the amplitude of the respiratory movements.

It may be concluded from the experiments described that the branchial vessels of fishes contain receptors, capable of responding to changes in pressure, and leading to reflex effects on the activity of the heart and vessels and on the respiratory movements. An important factor determining the character of the reflex response from this reflexogenic zone is the strength of stimulation of the receptors. This is shown particularly clearly by a study of the reflex responses of the heart: strong stimulation causes inhibition of the rhythm and weak stimulation leads to a quickening of the heart rate. This fact is important not only in describing the function of the reflexogenic zone of the branchial vessels in fishes, but also in

understanding the mechanism of action of the vagus nerve on the heart. The peculiar innervation of the heart in fishes, and also the absence of an inhibitory tonus of the vagus nerves suggest that both inhibitory and stimulatory effects are brought about by means of an active influence of the vagus nerve on the heart, and thus contradict the notion of a specifically inhibitory function of the vagus.

## SUMMARY

The author studied the relation between the stimulation strength of the pressor receptors located in the gill blood vessels of fish and the character of the reflex responses of the heart, peripheral blood vessels, and respiration in them. It was demonstrated that with mildly stretched gill blood vessels the rhythm of the cardiac contractions increases, while with vigorous stretching it decreases. Since in fish there is heart tone along the vagus nerves, and the cardiac sympathetic innervation is absent, the reflex intensification of the heart rhythm evidently is caused by the active impulse action of the vagus nerve.

Gill vessel stretching of variable intensity may also cause constriction and dilatation of the intestinal vessels and various changes in respiratory motions.

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