NERVOUS REGULATION OF THE RHYTHM OF CARDIAC CONTRACTIONS IN FISH

COMMUNICATION I. THE EFFECT OF STIMULATION AND SECTION OF THE CARDIAC BRANCHES OF THE VAGUS ON CARDIAC RHYTHM

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The concept of a purely inhibitory function of parasympathetic nerves in the vertebrates which arose in the middle of the last century has been under review in recent years. M. G. Udelnov, in a series of communications [3, 4, 5], has shown that both inhibitory and stimulating influences on the heart are mediated by the vagus. It has been established that both regulatory effects are mediated by similar parasympathetic elements. Inhibition or stimulation of cardiac activity is determined, as demonstrated by Udelnov's experiments, by the number of parasympathetic nervous elements whose impulses impinge simultaneously on the heart. When a relatively small number of vagal nervous elements are stimulated cardiac activity is enhanced, when a larger number of such elements is stimulated inhibition takes place. These data were obtained on animals (predominantly amphibia) which had both parasympathetic and sympathetic innervation of the heart, but the results remained unchanged if the experimental animals were subjected to preliminary sympathetic denervation of the heart. It appeared to be important to discover whether the vagi in animals lacking sympathetic innervation of the heart had the power to stimulate automatic cardiac activity.

In the cyclostomata the sympathetic trunk is absent [15], in myxine and in minnowlarvae there is no innervation of the heart at all [11]. Fish have a well-defined sympathetic chain, starting from the tail segments and reaching the level of the III-IV thoracic vertebrae [15]. Sympathetic nerves innervate many viscera in many cases although, according to Stannius [15], who investigated over one hundred species of various fish, no nerve fibers of sympathetic origin approach the heart. These data were repeatedly confirmed in more recent studies by morphologists and physiologists [9, 10 et al].

V. A. Shidlovsky [6], who carried out simultaneous recording of venous sinus, atrial and ventricular contractions in some bony fish, observed that on stimulation of the sympathetic "border" trunk a small positive inotropic effect on the venous sinus was seen; however, neither the rhythm of contractions of this structure nor any indicators of the activity of the other parts of the heart showed any changes in the fish examined by him. The venous sinus in these fish is a subservient section of the heart, since the leading cardiac bundle in their case is in the atrial auricle. If this is considered together with the absence of changes in the activity of the atria and ventricles in this case, then it must be recognized that this author, too, confirmed the absence of functionally active sympathetic innervation of the heart in fish.

A number of investigators [1, 2, 8, 9, 10, 12, 13, 14, 15] observed cardiac arrest on direct stimulation of the vagi in fish. According to these authors no stimulation of the heart beat was seen either during stimulation itself or subsequently, following arrest evoked by vagal stimulation. This permitted Skramlik [12, 13, 14] to

formulate his theory of unilateral regulation of the heart in fish, mediated by reflex changes in the inhibitory tonus of the vagi. According to his concepts, acceleration of the heart in fish does not occur as the result of active impulses from the vagi but from weakening of impulses from these specifically inhibitory nerves.

It can be concluded from the data available in the literature that fish are a very convenient object for the experimental solution of the problem whether active vagal influence on the heart devoid of sympathetic innervation can cause acceleration of the heart rate.

METHODS

The work was carried out at the Shcherbakovsky water reservoir in July-September 1949 and January-February 1950. Sixty short experiments on fish were performed: mainly on pike, also on tench, perch, carp, groundling bream and nalim *. No significant differences in the innervation of the heart were found in these fish.

The fish were taken from the water and fixed in a frame, on the back. The posterior part of the gill cover was removed, the membrane joining the shoulder girdle with the last gill arch was severed, the superficially lying nerve, a branch of the vagus in the fish, was dissected and traced to the root of the vagus. The other branches of the vagus were then dissected: 4 gill nerves, upper and lower pharyngeal nerves and the visceral branch. The cardiac branches (usually two on each side) may come off the visceral, pharyngeal or gill branches of the vagus; they enter the cardiac venous sinus with the ducts of Cuvier.

The abdominal wall was transected by a transverse incision at the level of the shoulder girdle; a second incision in the midline was made perpendicularly to the first and towards the head. The abdominal wall muscles overlying the heart and the bones of the shoulder girdle were removed. The heart was freed from the pericardium, a serrefine was applied to the apex and connected to an Engelman lever. Cardiac contractions were recorded on a smoked kymograph.

The distal end of one of the cardiac nerves was placed on stimulating electrodes connected through a switch to an induction apparatus.

RESULTS

On stimulation of the peripheral ends of the cardiac nerves of fish with induction currents of different strength various changes in cardiac activity were observed.

In some cases more or less prolonged cardiac arrest was seen (Fig. 1) which was usually replaced, still on the background of stimulation of the cardiac nerve, by cardiac contractions, first infrequent, then increasingly frequent (Fig. 1, b, c) – the so-called "phenomenon of cardiac escape from vagal influence." On cessation of stimulation the slowed rhythm of cardiac contractions sometimes returned immediately to normal (Fig. 1, a), but usually this was preceded by considerable acceleration of the heart rate and only after that was the initial rhythm of cardiac activity regained (Fig. 1, b, c). This is constantly observed in experiments on animals which possess both vagal and sympathetic innervation of the heart. It is explained as a result of the entry into the reaction of sympathetic cardiac nerves and is called "sympathetic after-effect." Neither this name nor the explanation cited above can be applied in the given case, since there is no sympathetic innervation of the heart in i...

In other cases stimulation of the cardiac branches of the vagi caused only more or less pronounced slowing of the heart rate (Fig. 2).

Finally, in a number of cases stimulation of the cardiac branches of the vagi led to acceleration of the heart rate (Fig. 3). Since acceleration of the heart rate elicited in animals lacking sympathetic innervation of the heart was in these experiments determined by stimulation of the peripheral ends of the cardiac branches of the vagus, explanation of this phenomenon by Skramlik's theory cannot be accepted.

This fact poses the question as to whether inhibitory tonic action of the vagus on the heart exists in fish. Skramlik's concepts were based on the results of his experiments with section of the vagi in fish which caused acceleration of the heart rate.

* A bony fish native to the USSR.

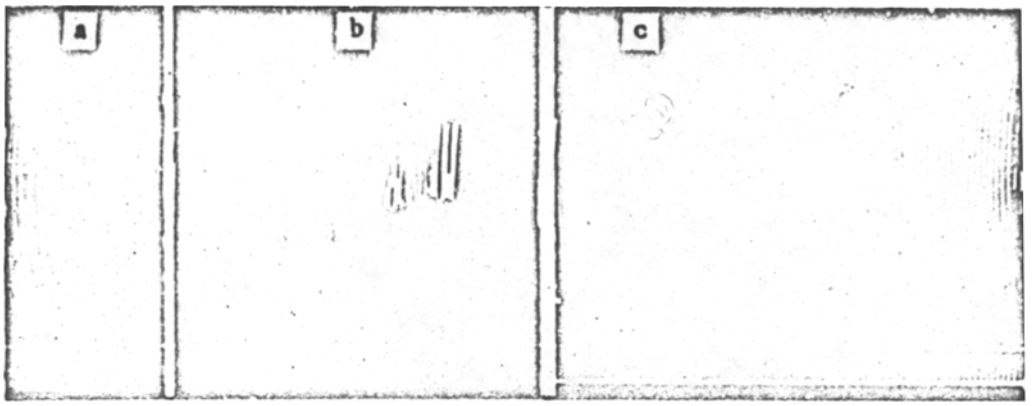

Fig. 1. Cardiac arrest (fish) in response to stimulation of the cardiac branches of the vagus. After cessation of stimulation the heart rate either immediately returns to the initial (a), or exceeds it slightly (b) or very markedly (c), then returning to the initial value. Records from above down: cardiac mechanogram, stimulus mark. Figures indicate distance between the induction coils during given stimulation; time marker.

Fig. 2. Slowing of the heart rate (fish) in response to stimulation of the cardiac branch of the vagus. Records the same as in Fig. 1.

Fig. 3. Sharp increase of heart rate during stimulation of the cardiac branch of the vagus. Records the same as in Fig. 1.

In a special series of experiments bilateral transection of the cardiac branches of the vagi was performed. As a rule, no changes in cardiac activity were associated with this. Such results were obtained in 23 of the 30 experiments carried out; in 3 cases transient acceleration and in four – slowing of the heart rate were observed. Comparable results were obtained by A. G. Filippova (1940). The results of the 7 experiments in which denervation of the heart was associated with transient changes in the rhythm of cardiac contractions can be regarded as a consequence of the stimulating effect of the transection of the cardiac branches, particularly since in the previous series of experiments both acceleration and slowing of the heart rate under the influence of electric stimulation of these branches of the vagus had been observed by the present author. It is possible that the acceleration of the heart rate observed by Skramlik also arose under the influence of a definite degree of stimulation, determined by the method adopted by him for the transection of the branches of the vagus. Skramlik does not mention the duration of the changes associated with this. The factual material presented suggests that the presence of sympathetic innervation of the heart or of inhibitory tonus of the vagi is not obligatory for the appearance of a positive chronotropic influence on the heart. Nervous regulation of the rhythm of cardiac activity can be achieved in these animals by means of active vagal influences in the same way as that which has been found by M. G. Udelnov to prevail in higher vertebrates possessing sympathetic innervation of the heart.

Acceleration of the heart rate, as well as slight slowing, occurred on stimulation of the cardiac nerves in fish within a very narrow range of variation in the strength of stimulating current exceeding only slightly the threshold value. It was at times sufficient to alter the intercoil distance by fractions of a centimeter only to be able to observe the reversal of effect; further increase in the strength of stimulation led to temporary cardiac arrest which occurred over a very wide range of changes in current strength and this particular form of vagal influence was thus easily elicited under the given experimental conditions. It may be thought that prolonged cardiac arrest occurs very infrequently under normal physiologic conditions and that the changing requirements of the fish organism can be satisfied by relatively small changes of cardiac activity in one or the other direction. The ease with which extreme, one might say freakish, forms of nervous activity influence cardiac function may explain why Skramlik and other authors failed to observe acceleration of the heart rate in fish on electric stimulation of the peripheral ends of the vagus. Al the data presented contradict Skramlik's concepts regarding the mechanism of functional regulation of the heart in fish and permit the assumption that both inhibitory and stimulating effects of the nervous sytem on the heart rate in fish are achieved as the result of active vagal influences.

SUMMARY

The results of sixty experiments on bony fishes, mostly pike , with stimulation of the peripheral ends of the cardiac branches of vagal nerves are reported. Frequency of heart contractions varied in accordance with the intensity of stimulation: in one and the same experiment the heart would stand still, slow down and hasten its contractions. Bilateral section of the cardiac branches of vagal nerves would cause transient changes of heart contractions in some cases, but no change whatsoever in most of them. Skramlik's theory on the tonus of vagal nerves in fishes must be revised to include the possibility of an active positive chronotropic effect of vagal nerves.

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