THE REFLEX NATURE OF THE PERIODIC GASTRIC HUNGER CONTRACTIONS

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Trnaslated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 50,
No. 11, pp. 23-28, November, 1960
Original article submitted January 18, 1960

Despite the large number of investigations of the nature of the periodic hunger contractions of the digestive system, much work remains to be done. The great majority of investigators consider them to be induced by some humoral influence acting both on certain central nervous structures [7, 14] as well as directly on the effector endings of the vagus and sympathetic nerves supplying the muscles of the gastrointestinal tract [1, 4, 6, 9, 12, 13, 16].

Carlson [15] associated the phasic activity of the empty stomach with the activity of the local nervous apparatus of the gastric wall. N. V. Raeva and L. K. Pupko [8], M. V. Tetyaveva [11], V. N. Ivanov [3], and N. N. Lebedev [5] attribute the periodic gastric contractions to the activity of the local nervous apparatus as influenced by a tonic inflow from the vagi.

The fact that the contractions are altered by division or by stimulation of the nerves supplying the stomach emphasises the importance of the part played by these nerves.

There are numerous references to the stimulating effect of the vagi on the activity of the empty stomach. However, the problem as to whether this activity is determined by naturally occurring afferent impulses passing along the vagi from the digestive tract has not previously been investigated.

In the present work we have determined the effect on the periodic gastric hunger contractions of the flow of afferent impulses reaching the vagal nucleus.

We have shown previously that it is possible to induce gastric contractions at periods when they would not normally occur, by artificially stimulating with sodium chloride solutions the receptors of the vagus after they had been associated with the skin by a nervous anastomosis with the vagus medianus. However, this method gave only indirect information concerning the parts played by afferent vagal fibers in the generation of gastric hunger contractions. The present work represents an attempt to establish directly the part played by the naturally occuring afferent vagal impulses in stimulating these contractions.

METHOD

The experiments were carried out on three dogs. All were supplied with gastric fistulae and a balloon, and the gastric contractions were recorded by the usual method. In addition, in each dog an anastomosis was made between the central end of the right vagus and the peripheral end of one of the nerves of the front legs [2]. The left vagosympathetic trunk in the neck was brought out into a strip of skin. In two dogs the skin strip contained the right vagosympathetic trunk above the site of anastomosis.

The left vagosympathetic trunk was contained in a portion of skin, and so could be blocked at any moment, and in all the animals the right vagus had been divided either mechanically or chemically. Mechanical block

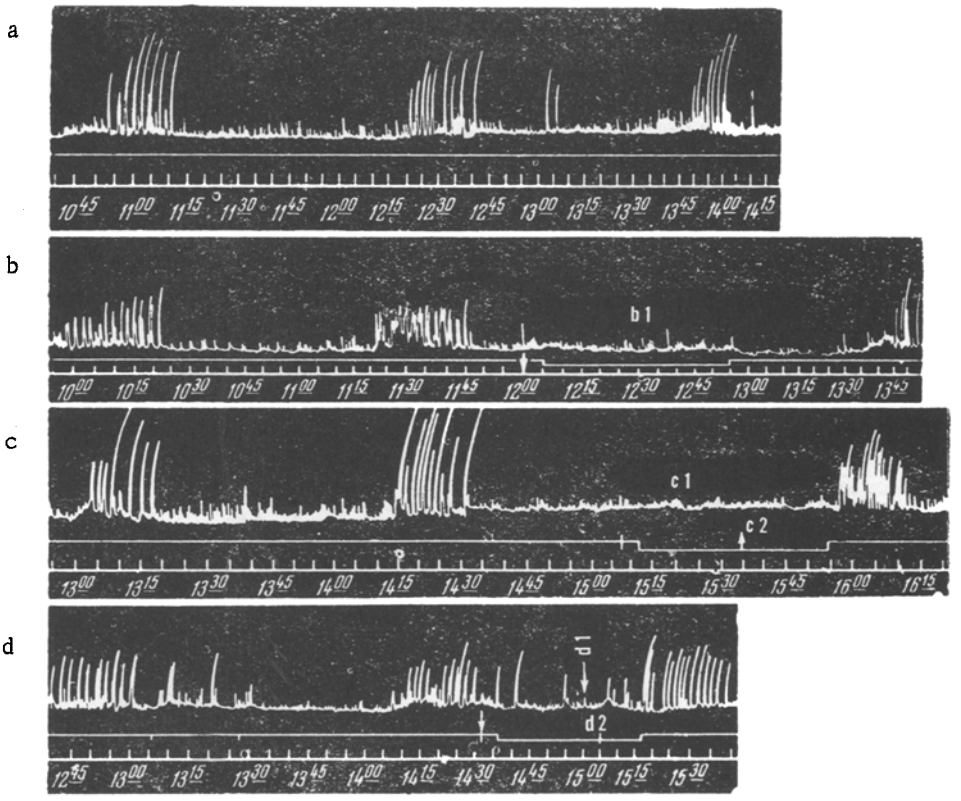

Fig. 1. Change in the gastric contractions following mechanical block of the remaining left vagosympathetic trunk. a) Initial rhythmic gastric hunger contractions; b) block established at the beginning of a resting period; c) block established at the end of a resting period; d) stimulation of the receptors of the right anastomosed vagus nerve, combined with block of the right vagus at the beginning of a resting period.
Key: b1) Reduction of the left vagus; c1) predominance of the left vagus nerve trunk; c2) P_s 200 in 1' Horner' syndrome; d1) Horner's syndrome from the left P_s 200 in 1'; d2) predominance of left vagus nerve trunk, 5% NaCl.

was made by applying pressure to the nerve by an inflated rubber cuff contained within a metal ring round the skin bridge. Usually a complete block occurred after 15-20 minutes of applying an air pressure of 120 mm mercury to the inside of the cuff. The onset of complete block was usually determined by observing the development of Horner's syndrome, and an increase of pulse frequency to 200 beats per minute.

Chemical block was induced by injecting 30 ml of 0.5% warmed novocaine solution into the nerve trunk. The dogs were starved for not less than 18-20 hours before the experiment.

RESULTS

First of all, in each animal the normal periodic hunger contractions were recorded. In two of them (Charley and Klyuchik) the active periods lasted on average for 15-20 minutes, alternating with periods of rest lasting for one hour (Fig. 1a). In the dog Ezhik, twenty-minute active periods were separated by intervals of one and a half hours.

In the first set of experiments a mechanical block was applied to the vagosympathetic trunk brought out into a strip of skin on the neck. It was found that the effect of such a block on the onset of gastric contractions depended on the moment of the resting period during which it was applied. If the pressure was applied at the beginning of a resting period, then the next active phase did not occur after the release of the block for a time equal to the length of a normal resting period (Fig. 1b). When a mechanical block was established in the middle of a resting period, the next active phase developed at a time after the release of the block equal to the difference

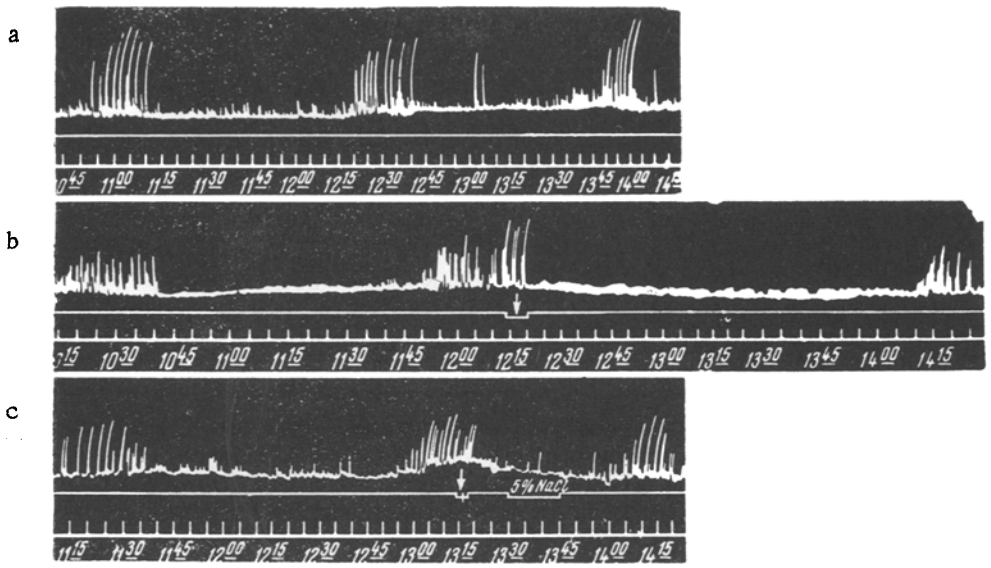

Fig. 2. Change in gastric motility in a dog following novocaine block on the left vagosympathetic trunk. a) Initial rate of gastric contraction; b) injection of 10 mg per kg of a 0.5% novocaine solution into the skin strip of the left side; c) stimulation of the receptors of the right anastomosed vagus by application of a 5% sodium chloride solution to the skin while applying a novocaine block to the left vagus.

between the normal duration of the resting period and the time which had elapsed between the end of the previous active period and the application of pressure to the nerve. However, when the block was established towards the end of a resting period and 15-20 minutes before the onset of the next contraction phase, the next period due occurred immediately after the block was removed (Fig. 1c).

It might be thought that one of the possible reasons for the delay in the operation of the mechanical block applied to the single remaining vagosympathetic trunk, when established at the beginning of a resting period, would be the stimulating effect of the block both on central nervous structures as well as directly on the gastric motor apparatus. However, the fact that mechanical block established at the end of a resting period did not prevent the development of hunger contractions from occurring after it had been removed, demonstrates in our opinion that such a procedure exerts no inhibitory effect on gastric contractions. All the same, special control experiments were arranged to check this point. In the dog Ezhik, the block was established on the trunk of the right anastomosed vagus which was brought out into a similar strip of skin. The left vagosympathetic trunk then remained intact. When the anastomosed vagosympathetic trunk was blocked, no changes were observed in either the type or the rate of the gastric contractions.

It seems to us that these control experiments exclude any possible direct stimulant action on a nervous center by the block itself. It must also be supposed that the stimulant effects of any mechanical stretching of the vagosympathetic trunk must have been prevented by the previous injection into it of 2 ml of a 2% novocaine solution, which was given in every case when the mechanical block was applied.

In our opinion the delay in the onset of the next set of gastric contractions which occurs when the block is applied at the beginning of a resting period was due to the arrest of afferent impulses passing along the vagus from the gastrointestinal trunk to the vagal center. As confirmation, it was decided to block the current of afferent impulses to the vagal nucleus during a resting period. For these purposes, during a block of the left vagosympathetic trunk the receptors of the right vagus were stimulated in the skin by a 5% sodium chloride solution. The effect was that a period of gastric contractions usually occurred immediately after withdrawal of the block (Fig. 1d).

These experiments have therefore shown that a mechanical block of the vagus established at the beginning of a resting period prevented the flow of afferent impulses to the vagal nucleus, which in turn prevented the return of excitability of the central vagal apparatus. It is only when the nerve block was removed, and when the

flow of afferent impulses to the center was restored that its excitability once more began to return to the critical point beyond which efferent discharges were distributed to the periphery. At the end of a resting period, the center had probably succeeded in becoming "charged" into its operating state, so that vagal block at this period prevented only the spread of efferent impulses to the periphery.

In the second set of experiments an attempt was made to eliminate the conduction of afferent vagal fibers during a certain time interval. For this purpose a novocaine vagosympathetic block was used; 10 mg per kg of a 0.5% solution of novocaine was injected into a portion of skin.

Control experiments showed that this procedure effectively produced a selective block of the afferent vagal fibers only. Thus, when the novocaine solution was injected into the portion of skin containing the right anastomosed vagus nerve, for the next 30-50 minutes it was not possible to obtain the normal reflex response to stimulation of the cutaneous vagal receptors which normally takes the form of coughing or vomitting in response to chemical stimulation [2]. However, the leg continued to move in conjunction with the act of swallowing and respiration, which showed that the continuity of the efferent fibers of the anastomosed vagus were intact.

When a 0.5% novocaine solution was injected into the strip of skin containing the single remaining intact left vagus nerve, there was a delay of 30-50 minutes in the occurrence of the next set of gastric contractions (Fig. 2b).

Special experiments showed that during this procedure the excitability of the vagal nucleus to stimulation of the receptors of the right anastomosed vagus was not changed. In response to stimulation of the receptors of the right vagus with 5% sodium chloride solution during novocaine block of the left vagus, a set of gastric contractions was initiated out of its normal turn (Fig. 2c). These experiments showed that the conductivity of the efferent fibers was maintained during novocaine block of the single remaining vagus nerve. It follows therefore that the observed delay in the occurrence of the next set of gastric contractions which follows novocaine block of the single intact left vagus may be due principally to suppression of conduction in its afferent fibers.

In our opinion the results indicate definitely that afferent impulses passsing along the vagal fibers during the resting period are concerned in the development of the periodic gastric motility.

On the one hand, by stimulation of the vagal receptors, which causes an additional flow of afferent impulses into the vagal center we have been able to cause a set of gastric contractions to occur out of their normal turn [10]; on the other hand, selective block of the vagal afferent fibers has been shown to cause a delay in the appearance of the contractions.

The part played by humoral influences is apparently of secondary importance. Indeed, if the periods of excitation of the vagal nucleus were induced by humoral factors, then when the efferent vagal fibers were conducting, gastric hunger contractions ought always to occur. But in fact they do not, as can be seen from the experiments described above.

When there is hunger, the humoral factors very likely determine merely the initial level of excitation of the central nervous structures. The periodic processes of excitation which occur in the vagal nucleus are elaborated under the influence of afferent impulses from the gastrointestinal tract passing to the center along the vagi.

SUMMARY

A study has been made of the mechanism of the periodic gastric hunger contractions. An anastomosis was made between the central portion of the right vagus and the peripheral end of one of the nerves of the forelimb. Cutaneous receptors of the right vagus nerve were stimulated; the left vagus nerve was brought out into a skin bridge on the neck, and a mechanical and a novocaine block was established. The results indicate that afferent impulses in the vagi are concerned in stimulating gastric hunger contractions.

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