

DEVELOPMENT OF THE MOTOR INNERVATION OF THE MUSCULATURE OF VARIOUS PORTIONS OF THE RAT STOMACH IN ONTOGENESIS

COMMUNICATION II. ONTOGENESIS OF THE DIFFERENTIAL INFLUENCE OF THE VAGUS ON GASTRIC SMOOTH MUSCLE

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In a study of postnatal development of motor function in the smooth muscle of the stomach the rate it has been shown that in the muscle in all portions of the stomach there is a gradual transition from the initial uniform tonic activity to a specialized form of contraction [1]. In rats vagotomized at various developmental periods it was shown that the fibres of the vagus have a different functional significance in different regions of the stomach and play an essential part in the development and differentiation of their activity [3].

In the present work we have made a study of the response of the musculature of the various parts of the stomach to electrical stimulation of the peripheral end of the vagus at various post natal periods.

Most authors, in studying the influence of electrical stimulus of the vagus on the musculature of the gastrointestinal tracts, either in the adult or in the post natal period, have noticed that it exerts an excitatory influence [4-11, 13]. However, in certain investigations on birds it was found that stimulation of these nerves is associated with inhibition and with a biphasic response of the musculature, depending upon the original condition of the organ [12, 14].

The present investigations were made by a method in which a record was made of the response of the stomach as a whole. The method we have used enabled a simultaneous in situ recording to be made of the activity of the musculature of the three divisions of the stomach, and so allowed their response to vagal stimulation to be separately determined.

METHOD

Acute experiments were carried out on rats of all ages from a few hours to maturity. Most of the experiments were made on animals at stages which had previously been shown to be critical in the development of the functional properties of gastric smooth muscles. They were anesthetized with $0.8 + 1.0$ g per kg methane. The vagus was exposed over the first third of its length on the right and the left side. The nerves were ligated and divided. The abdominal cavity was then opened along the midline, the stomach was exposed, and each division along the greater curvature was fixed on a glass tube bent at right angles, held in a stand. In the corresponding (fundal cardiac and pyloric) portions threads were fixed along the lesser curvature, and their free ends were connected to a light myograph.

To perform the experiment the animal was placed on a "chaise longue" support, was immersed up to the thorax in a bath containing Tyrode's solution at 38° , or was placed on a plate kept warm by an electric lamp. In the latter case the stomach was periodically moistened with Tyrode solution ($37-38^{\circ}$).

The vagus was stimulated by potentials from a Dubois-Reymond induction apparatus connected to platinum electrodes separated by 1-2 mm. The stimulus periods varied from 30 to 90 seconds with an interval of 8-15 minutes. In each experiment the threshold stimulus was determined and the optimal stimulus strength determined.

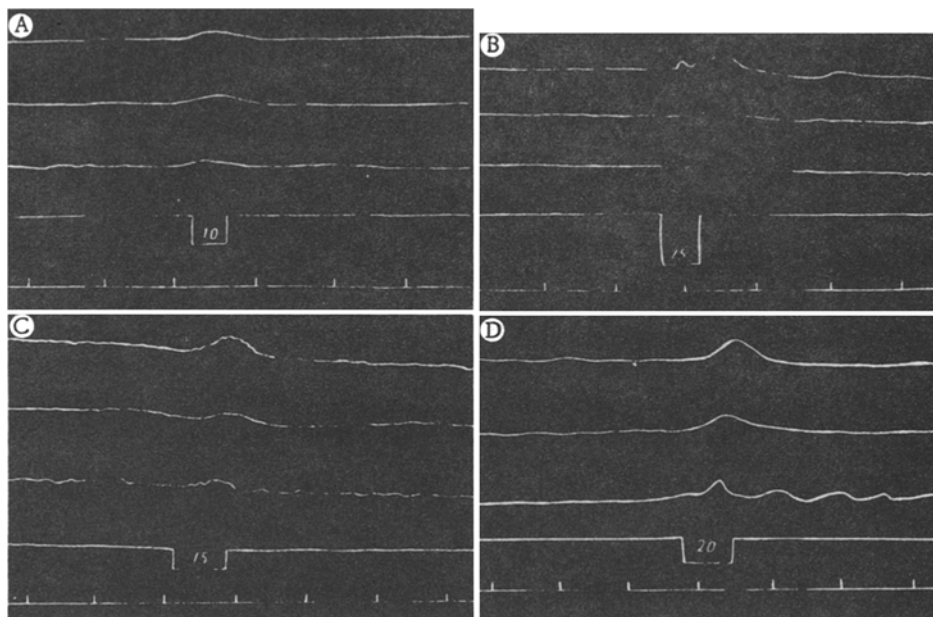


Fig. 1. Motor response of the smooth muscle of different parts of the rat stomach to stimulation of the peripheral end of the vagus in the neck during the postnatal period (from the first to the fifteenth day of life). A) One-day; B) eight-day; C) twelve-day; D) fifteen-day rat. Curves, from above downwards; myographic record of the response of the musculature of the fundal, cardiac, and pyloric regions of the stomach; stimulus marker; time marker (one minute). The figures on the stimulus line represent the distance between the induction coils in cm.

In most experiments the stimulus was applied to the right vagus. However, we found no difference in the effect on the muscle between stimulation of the right or the left vagus.

EXPERIMENTAL RESULTS

Stimulation of the peripheral end of the vagus in the neck of an adult rat caused marked differences in the muscular contractions; there was a strong contraction of the fundus, and rapid rhythmical contractions occurred in the pyloric region (Fig. 2F). The response in the cardiac region resembled that of the fundal and pyloric parts.

In the first days of life vagal stimulation caused nothing but a tonic muscular contraction developing slowly in all parts of the stomach, a result which contrasted with the response in adults (Fig. 1A). At this age the response was variable. The latent period varied between 10 and 45 seconds, and was often influenced by the strength of the current.

For different animals of the same age the stimulus threshold varied from 35 to 17 cm separation of the coils. Usually the excitability of the nerve was depressed after the first stimulations, and when subsequently more prolonged and stronger stimuli were applied the response occurred only after a certain delay. However, the nature of the response characteristics of this age depended on neither the strength nor the duration of the stimulus applied to the nerve.

After the age of one week, contractions of all the regions of the stomach occurred more frequently in response to vagal stimulation (Fig. 1B, C). Subsequently, rhythmical contractions of these fundal regions were gradually restricted and were replaced by tonic contraction, whereas in the pyloric regions phasic activity increased still further.

In animals aged two weeks we observed that differentiation in response to vagal stimulation first occurred in all parts of the stomach. The fundal and cardiac regions responded by contraction and the pyloric region by a simple contraction of moderate strength followed by a series of rhythmical tonic movements (Fig. 1E). The effects were still feebly shown and represented the initial stage in the formation of different types of motor response in the different regions.

Figure 2 illustrates the subsequent course of the formation of specialized responses. In 17-day-old rats (Fig. 2A) the differentiation of the response was already marked, and was shown by contractions in the fundal and cardiac regions

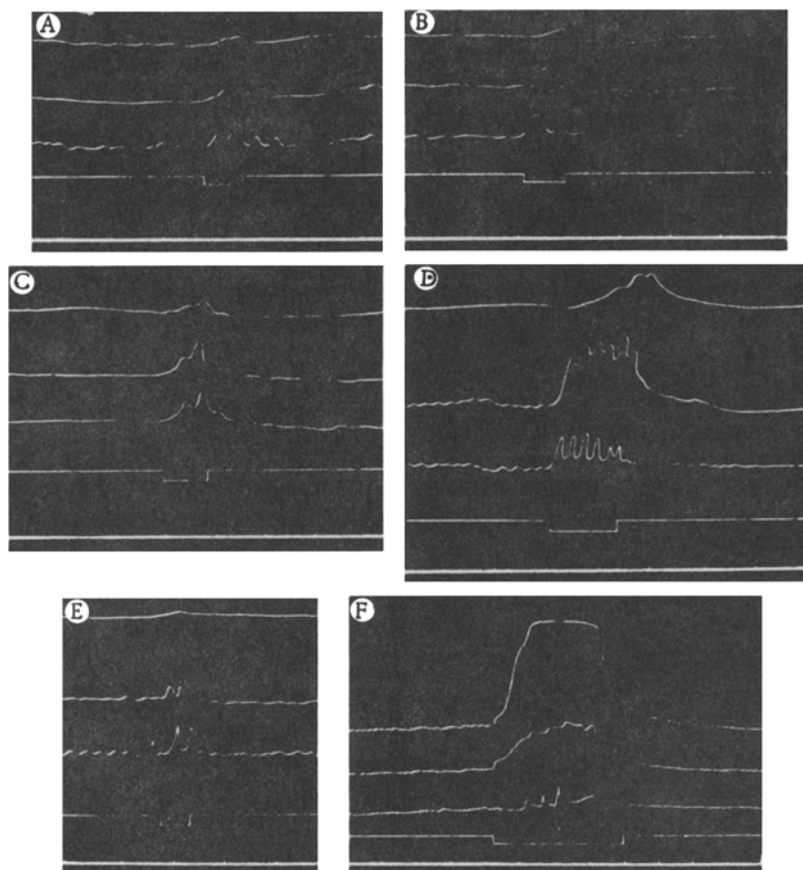


Fig. 2. Differentiation of the response of the musculature of the different regions of the rat stomach to stimulation of the peripheral end of the vagus in the neck, during the postnatal period (from the seventeenth day after birth to maturity). Rat aged A) seventeen days; B) nineteen days; C) thirty days; D) two and a half months; E) three months; F) eight months. Remaining indications as in Fig. 1.

and by a group of weak movements of long duration in the pyloric region. These differences between the different parts increased with age, becoming more noticeable (Fig. 2B, C).

In animals aged three to four weeks the latent period of the reaction was shortened to 1-3 seconds, or else was not noticeable. The stimulus thresholds were reduced, and in rats aged one month became stable at a separation of 40 cm of the coils. At a later stage, in animals aged two to three months (Fig. 2D, E) the response of the musculature to vagal stimulation became entirely specialized in the different parts of the stomach, and corresponded to the adult response. The extent of the tonic reaction of the fundal region might vary according to the initial condition of the substrate.

We should notice the resemblance during rat ontogenesis between the response of the gastric musculature to vagal stimulation and to the action of acetylcholine [2].

From the results of these experiments it follows that during the postnatal period the influence of the vagus upon the muscles of the different parts of the stomach becomes increasingly differentiated and develops finally into the specialized activities of these regions.

SUMMARY

From the first day after birth to the age of two weeks stimulation of the vagus nerve caused a uniform tonic reaction — a weak contracture in all portions of the stomach. From the age of 2 weeks there appear manifestations of divergent relationships between different portions of the stomach becoming ever more considerable. The tonic activity

increases in the fundal portion, and rapid rhythmic contractions — in the pyloric one. Thus, the effect produced by the vagus on the functional properties of the smooth muscles in rat ontogenesis is involved in elaboration and specialization of the activity of musculature in each of the stomach portions.

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