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**A STUDY OF GASTRIC STRETCH RECEPTORS. THEIR ROLE
IN THE PERIPHERAL MECHANISM OF SATIATION OF
HUNGER AND THIRST**

BY A. S. PAINTAL*

*From the Physiology Branch, Technical Development Establishment
Laboratories, Kanpur, India*

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A number of investigators have shown that reflex respiratory, pupillary or vascular effects are produced by stimulating the central end of the vagi below the diaphragm (Brodie & Russell, 1900; Neumann, 1914; Carlson & Luckhardt, 1921; Harper, McSwiney & Suffolk, 1935), although these observations do not indicate that nerve fibres of the stomach are involved. However, Irving, McSwiney & Suffolk (1937) have shown clearly from a study of pupillary responses that sensory impulses in the vagus are produced when the stomach is distended.

The presence of myelinated afferent fibres in the vagus at the level of the diaphragm was pointed out by Edgeworth (1892) and confirmed by Langley (1892). Evidence for spindle-shaped endings in the stomach has been provided by the histological studies of Langworthy & Ortega (1943) who showed that they are connected to myelinated fibres thought to be sensory in function.

In spite of these studies, impulses from afferent fibres of the stomach have been recorded only recently (Paintal, 1953*c*). These were in fact found in the course of an investigation into the normal function of receptors stimulated by phenyl diguanide (Paintal, 1954*a*). Since then these gastric stretch receptors have been studied further, and several interesting facts regarding their responses to mechanical stimuli and drugs have emerged. Their responses to drugs are described in another paper (Paintal, 1954*b*).

Recent studies (Janowitz & Grossman, 1949; Share, Martyniuk & Grossman, 1952) have shown conclusively that food intake in dogs is influenced to a large extent by distension of the stomach whether the distension is achieved mechanically by a balloon or by calorically inert food. Further, distension of the stomach with a water-filled balloon inhibits sham drinking, a reflex that is

* Present address: Vallabhbhai Patel Chest Institute, University of Delhi, Delhi, India.

abolished by vagotomy (Towbin, 1949). There is thus clear evidence for the existence of a peripheral sensory mechanism of satiation of hunger and thirst. The results of the present investigation provide evidence for the existence of such a sensory mechanism that must certainly be operative during distension of the stomach.

METHODS

Experiments were performed on nineteen adult cats, weighing 1.5–3.7 kg, anaesthetized with intravenous injection of chloralose (70 mg/kg) after induction with ether. Gastric afferent fibres could be isolated in fifteen cats only. The recording apparatus and the method of isolation of single units from the right cervical vagus were identical with those described previously (Paintal, 1953*b*). As before, a binocular travelling dissecting microscope served as an invaluable aid in the dissection of nerve fibres. Although the isolation of gastric stretch fibres was always much more difficult than the isolation of pulmonary and cardiovascular afferent fibres, the procedure was made considerably easier by inserting a balloon into the stomach before the dissection of the vagus was begun. This balloon consisted of a teatless condom 6 in. long tied to a glass tube. In the earlier experiments it was inserted through an incision in the duodenum and the tube held in place by a ligature tied round the duodenum. By means of a T-piece this was connected on one side to a mirror membrane manometer and on the other to a short length of rubber tubing. Distensions of unknown volumes were obtained by blowing into the tubing, and graduated ones by pumping in air of known volumes and at known speeds with the aid of a respiratory pump.

The mirror membrane manometer served as a satisfactory signal for the distending force, but did not give a satisfactory indication of the progress of distension of the stomach which lagged behind a little. With the balloon connected only to the manometer, a satisfactory record of intra-gastric pressure was obtained.

In subsequent experiments, the balloon was inserted through the mouth. The diameter of rubber tubing connected to the condom had to be reduced, and this increased the resistance to inflation thereby reducing the rate of distension of the stomach. In these experiments, a similar balloon was also placed between the stomach and the diaphragm. This latter balloon was connected to the manometer and served as a satisfactory signal for respiratory movements and gastric distension. It was also used to distend the upper part of the abdomen when required.

After the insertion of the balloon, fine nerve strands from the vagus were dissected. These were hooked on to the recording electrodes one by one and their response to gastric distension noted till one was obtained which yielded an unmistakable discharge when the stomach was distended. This strand was subdivided further if necessary to eliminate other active units and was then unequivocally identified. In later experiments, the balloon was kept partially distended with air and the various strands examined for a persistent discharge. When one was encountered its response to gastric distension was noted as before. This procedure simplified the isolation of gastric afferent fibres in several experiments.

In the experiments where the balloon was inserted through the duodenum, the oesophagus was tied off low in the neck early in the experiment to prevent regurgitation of gastric juice when the stomach was distended. If this was not done, the gastric juice irritated the glottis leading to violent coughing which dislodged the fibres from the recording electrodes.

RESULTS

Identification of gastric stretch afferent fibres

In these fibres the discharge of impulses following distension of the stomach was, as a rule, so characteristic that little difficulty was experienced in distinguishing them from other afferent fibres in the vagus. Differentiation from

various cardiovascular afferent fibres was easily achieved as the patterns of discharge in gastric stretch afferent fibres never showed any superimposed cardiac rhythms. Except in one fibre no respiratory variations were observed in these afferent fibres and so distinction from normally active pulmonary stretch fibres was also quite easy. However, on some occasions differentiation of these gastric fibres from normally inactive pulmonary stretch fibres presented slight difficulty. These latter were of the type that gave a discharge of impulses when the stomach was distended (Fig. 1). It is well known that there are many pulmonary stretch receptors that are inactive during quiet respiration, and it

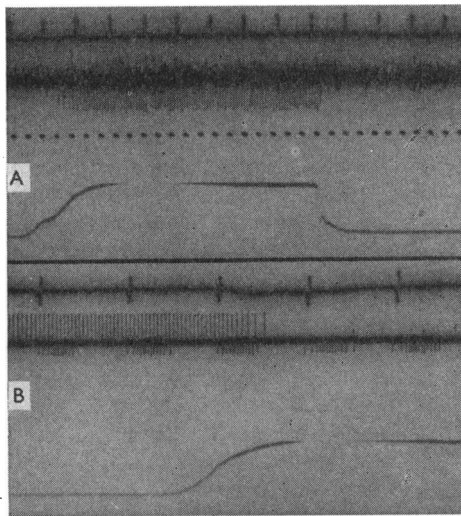


Fig. 1. Influence of gastric distension on the activity of two pulmonary stretch fibres. In A, gastric distension stimulates a pulmonary stretch fibre; in B, distension inhibits the discharge in another fibre. From above downwards in A and B, e.c.g.; record of impulses in vagal afferent fibres; time marks in $\frac{1}{16}$ sec (in A only) and distension signal.

is conceivable that raising the diaphragm by distension of the stomach would lead to a localized compression of the base of the lungs; this would be accompanied by stretching the neighbouring portions of the lungs which in turn would lead to stimulation of the previously inactive pulmonary receptors situated here. Distinction of these pulmonary fibres from gastric ones was obtained by noting the response of the fibres to inflation and deflation of the lungs which evoked the well-known responses from the slowly and rapidly adapting pulmonary stretch fibres. With a collapsed stomach none of the gastric fibres so far studied responded to inflation or deflation of the lungs. This test was carried out on all fibres suspected to arise from the stomach and if there was a positive response it was assumed that the fibre was of thoracic origin.

In many slowly adapting pulmonary stretch fibres distension of the stomach with about 100–200 ml. of air produced either a reduction or an increase in the discharge (Fig. 1). The increase was usually short-lived, but at times the discharge so produced was slowly adapting and was presumably due to the mechanical effect of the distension on the thoracic viscera produced by raising the diaphragm and widening the lower left portion of the chest.

Another way of distinguishing the gastric afferent fibres from the slowly adapting pulmonary stretch fibres was to note the response of the fibres to distension of the balloon placed between the stomach and the diaphragm.

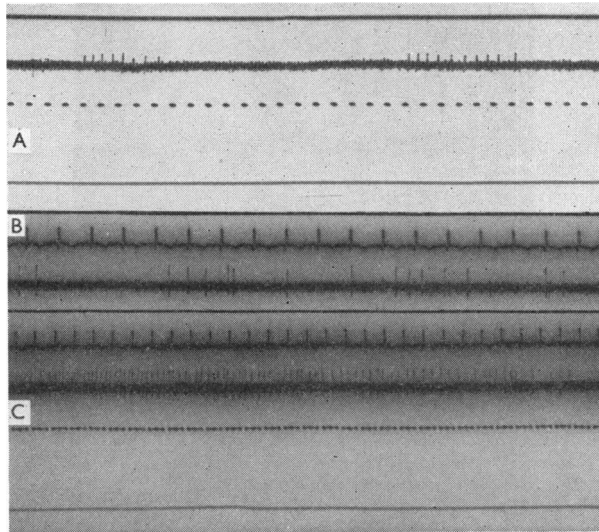


Fig. 2. Records of spontaneous discharges in two gastric stretch fibres. Records B and C are from the same fibre before and after injecting adrenaline intra-aortically. From above downwards in each, e.c.g.; impulses in gastric stretch fibres; (in A and C only) time in $\frac{1}{10}$ sec and record of intragastric pressure. The heart had stopped in A.

In pulmonary stretch fibres this yielded a response similar to that seen when the intragastric balloon was distended, while in gastric stretch fibres as a rule this had no effect (Fig. 4). However, in one fibre this manoeuvre yielded a small train of impulses which was in no way comparable to the characteristic slowly adapting discharge resulting from distension of the stomach. Since it is possible that there are vagal afferent fibres with endings in the peritoneum and other neighbouring abdominal viscera this procedure also helped to exclude these.

Additional confirmation about the identity of gastric stretch receptors was obtained by their characteristic response to an intra-aortic or intravenous

injection of phenyl diguanide (Paintal, 1954*b*). After making all the necessary observations most of the receptors were finally localized in the stomach by digital compression or by stretching of the stomach wall (Fig. 11).

Spontaneous discharges

Spontaneous activity, if any, was looked for carefully in twenty-five gastric stretch afferent fibres, but it was met with in only eight of them (Table 1). The pattern of discharge in each of these varied from fibre to fibre and in the same fibre at different times. In six fibres spontaneous activity consisted of irregular single impulses or bursts of impulses with a peak frequency varying from 1 to 38 impulses/sec during the bursts. Between bursts there were intervals lasting 1–10 sec of reduced or no activity.

TABLE 1. Characteristics of spontaneous discharges in eight gastric stretch afferent fibres

Fibre no.	Pattern of discharge	Impulses/sec		No. of impulses in groups	Frequency of groups (groups/min)	Situation of receptor
		Maximum	Minimum			
1	<i>S, G</i>	35	2	40	?	<i>C</i>
2	<i>S</i>	10	2	—	—	<i>P</i>
3	<i>S</i>	1	0	—	—	—
6	<i>S</i>	6	0	—	—	<i>B</i>
10	<i>G</i>	18	0	6–10	25–50	<i>P</i>
12	<i>S</i>	8	0	—	—	<i>P</i>
13	<i>G</i>	20	0	80–90	2	—
30	<i>S</i>	5	0	—	—	—

S, pattern of discharge consists of single irregular impulses; *G*, pattern of discharge consists of groups of impulses; *C*, cardiac end of stomach; *P*, pyloric end of stomach; *B*, body of stomach.

In fibre no. 1 the single impulses were accompanied by groups of impulses of 1.5–2 sec duration in which the peak frequency was much higher. In two fibres, only grouped discharges were seen (Fig. 2). One of these (no. 10, Table 1) showed groups of 6–10 impulses with a peak frequency of 18/sec in the groups. The groups which occurred at a variable frequency of 25–50/min had on no occasion any relation to respiratory or cardiovascular events. In the other fibre (no. 13, Table 1) spontaneous activity consisted initially of either single impulses or groups of three or four impulses, the groups occurring irregularly at a frequency of 30–40/min. At times for several seconds at a stretch there was no activity. After an intra-aortic injection of adrenaline, however, a rhythmic pattern of discharge appeared (Fig. 2). This consisted of groups of 80–90 impulses, each group occurring regularly at a frequency of about 2/min. The maximum frequency of impulses in each group was about 20/sec and between the groups there were no impulses (Fig. 3). The intra-gastric pressure remained constant throughout this period apart from the regular respiratory fluctuations in pressure which did not affect the activity of the fibre in any way.

A similar type of activity was observed in another fibre from a receptor which did not respond at all to distension of the stomach or to digital stretching

and compression of different parts of the stomach. This fibre yielded a discharge of impulses 1.4 sec after an intra-aortic injection of phenyl diguanide which indicated that it was located somewhere in the abdomen.

In those experiments where artificial respiration was used, the production of asphyxia by stopping the respiratory pump for 2 min caused no change in the spontaneous activity of a number of gastric stretch receptors. Further, in several experiments the responses of the receptors were studied after the heart had stopped for several minutes, occasionally for as long as half an hour. In no case, however, did spontaneous activity commence in receptors that had been inactive while the circulation was intact, or increase in those which showed spontaneous activity previously (Fig. 2). These receptors are, therefore, not sensitive to anoxia or CO₂ excess.

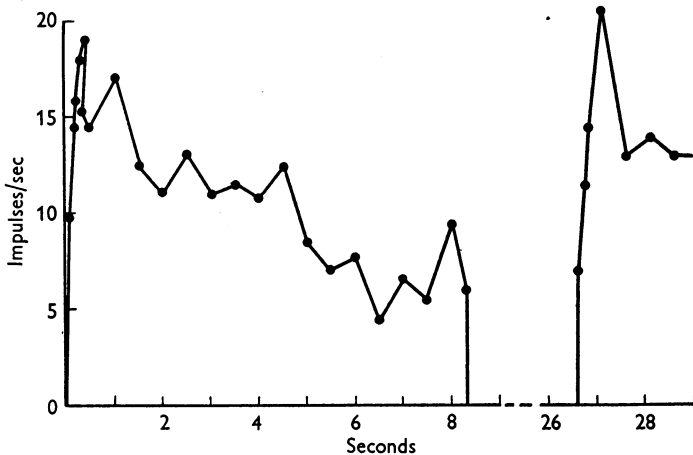


Fig. 3. Graph of spontaneous discharge in the gastric stretch fibre shown in Fig. 2 B and C after injection of adrenaline (60 $\mu\text{g}/\text{kg}$) into the abdominal aorta.

Table 1 shows that the lowest frequency of discharge found in all the fibres varied from 0 to 2 impulses/sec, and it is not difficult to imagine that if the activity in the fibres is studied mainly on the screen of the cathode-ray tube or over the loudspeaker, many of the impulses would be missed as is believed to have happened in an earlier investigation where it was concluded that phenyl diguanide receptors are normally inactive (Paintal, 1953*a*). Further, since it is comparatively more difficult to isolate single units of these fibres, their activity was masked by the more prominent discharges from pulmonary and cardiovascular afferent fibres which often accompany them in the small strands. These facts became apparent early in the investigation and, therefore, spontaneous activity was studied entirely from continuous photographic records taken at a slow speed over comparatively longer periods.

It has not been possible so far to relate the spontaneous discharges to any known phenomenon occurring in the stomach. Increased tone of the stomach produced by pouring a solution of acetylcholine over it or gastric contractions induced by electrical stimulation, resulting in increased intragastric pressure, did not produce any activity in fibres that were inactive when the stomach was atonic.

All the cats concerned in these experiments were starved overnight, and at the time of studying their spontaneous activity the condom in the stomach was kept deflated. The deflated volume of the condom was not more than 10 ml. Post-mortem examination confirmed that there was no food in the stomach and that the stomach was normal in all the cats. A small quantity of gastric juice was always present.

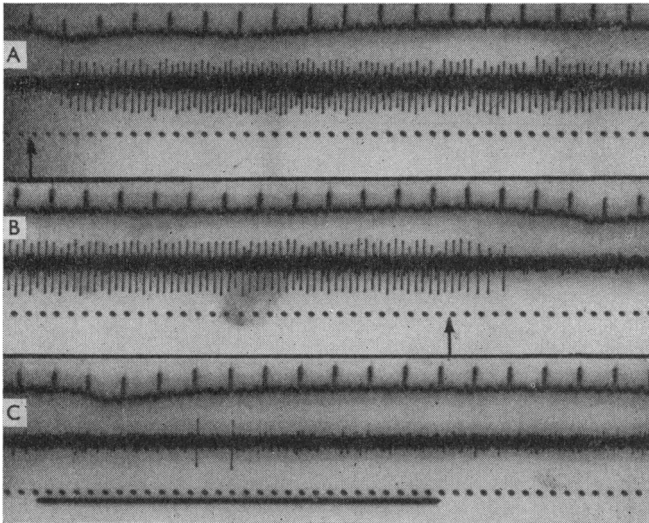


Fig. 4. Response of a gastric stretch receptor to a maintained distension of the stomach. At arrow in A 150 ml. of air was pumped in and the distension released at arrow in B. Record in B taken 70 sec after A. In C rapid distension of the balloon between the stomach and the diaphragm with 250 ml. of air during signal (last trace) has no effect. From above downwards in each, e.c.g.; impulses in a gastric stretch fibre, time in $\frac{1}{10}$ sec.

Responses to distension of the stomach

The responses of over a hundred gastric stretch receptors to distension of the stomach have been observed. In each fibre the discharge started about 0.1–0.5 sec after the beginning of the distension and ended after a slightly greater interval following the release of the distending force (Fig. 4). The increased delay was considered to be due to the inertia of the balloon.

The threshold of distension at which the receptors were stimulated varied

considerably in different fibres being anything from 5 to 150 ml. of air; in the majority the threshold was less than 50 ml. At times, in the same fibre, the threshold varied with the position of the balloon in the stomach, the position of the stomach in the abdomen and the tension exerted by instrumental attachments such as cannulae in the stomach. However, with the stomach *in situ*, the threshold remained constant throughout the period of observation. The threshold was not greatly affected by bringing the stomach out of the abdominal wound. The peak frequency of impulses attained with maximal distension varied between 25 and 60 impulses/sec in different fibres.

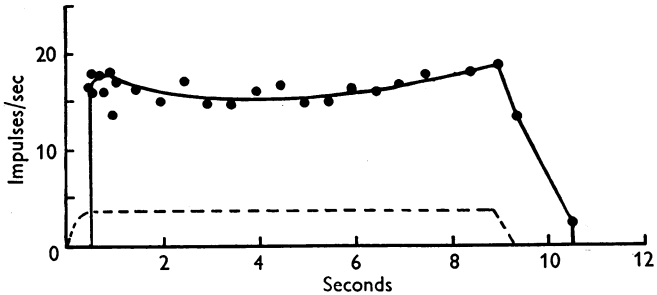


Fig. 5. Graph of response of a gastric stretch receptor to maintained distension of the stomach. The frequency after 9 sec is as high as the initial peak frequency following rapid distension of the stomach which is indicated by the interrupted line.

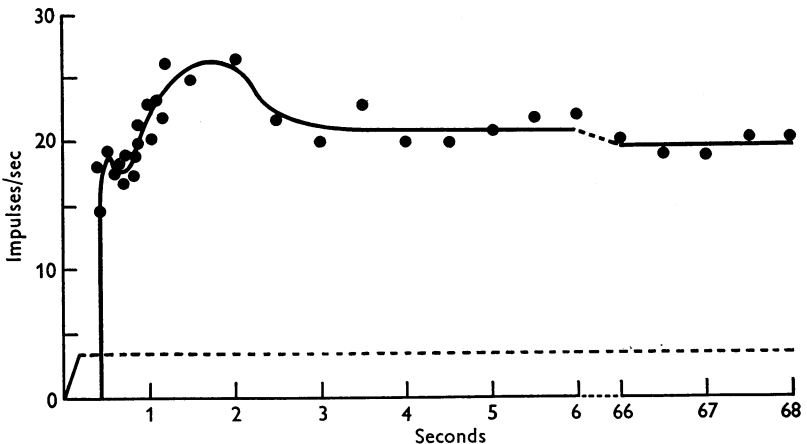


Fig. 6. Graph of response of a slowly adapting gastric stretch receptor to distension of the stomach which was maintained for over 1 min. Distension is indicated by the interrupted line.

Adaptation

A study of thirty gastric stretch receptors in detail showed that during a maintained distension, the discharge in the majority of the fibres tended to adapt slowly. In many, no tendency to adaptation was observed even with rapid and large inflations, the initial peak frequency in these being the same as

that several seconds later (Fig. 5). In one fibre a rapidly adapting type of discharge was observed (Fig. 7). This was unaffected by the position of the balloon in the stomach or by the relative position of the stomach in the abdomen. The threshold of this receptor was about 125 ml. of air and it was located very near the cardiac sphincter. It was confirmed that the rapidly adapting response was not due to the effect of anoxia on a slowly adapting type of receptor as observed by Adrian in pulmonary stretch fibres (1933).

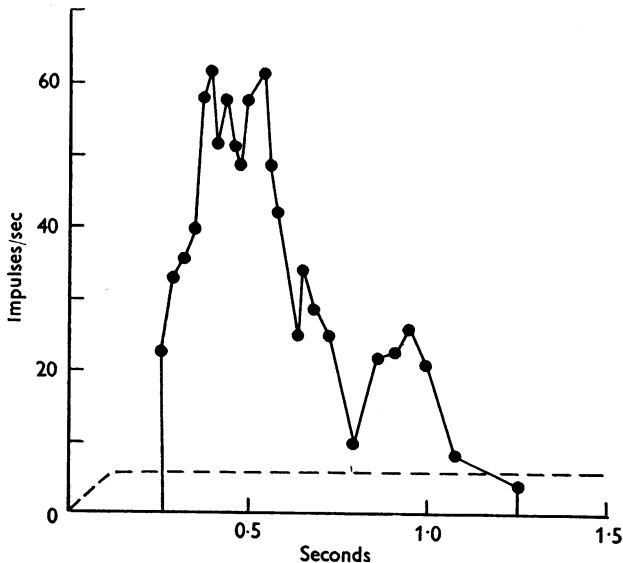


Fig. 7. Graph of response of a rapidly adapting gastric stretch receptor to rapid distension of the stomach with 200 ml. of air. Distension is indicated by the interrupted line.

Three other receptors located in the region of the cardiac sphincter showed the typical slowly adapting response. Another one, sensitive to phenyl diguanide and also located here, gave no response to gastric distension. It, therefore, appears that there is some variation in the nature of responses given by receptors at the cardiac end of the stomach. All those in the pyloric end of the stomach showed slowly adapting discharges. In a few fibres the distension was maintained for several minutes. In one of these, the discharge frequency was unaltered after several minutes; in another there was only a slight fall after 1 min (Fig. 6) and in the third the frequency fell by about 16% after a minute. These observations indicate that the gastric stretch receptors are capable of signalling the degree of distension of the stomach.

During a maintained distension of the stomach gastric contractions induced by an additional stimulus, e.g. galvanic current, had apparently no influence on the discharge although there was a considerable rise in intragastric pressure.

Further, respiratory fluctuations in intragastric pressure did not influence the discharge except in one case. However, manual compression of the distended stomach produced an increase in the discharge frequency in all cases, where this procedure was carried out (Fig. 8). This was presumably due to the increased stretching of the stomach at the site of the receptor. It is therefore

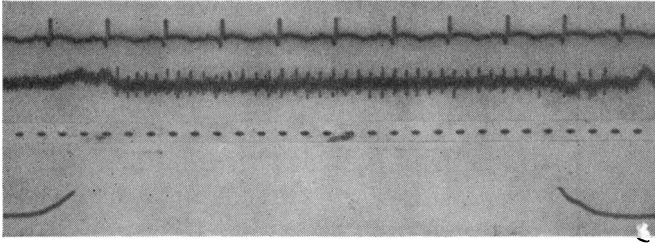


Fig. 8. Impulses in a gastric stretch afferent fibre following compression of partially distended stomach. From above downwards, e.c.g.; impulses in a gastric afferent fibre; time in $\frac{1}{10}$ sec; and intragastric pressure. The degree of distension of the stomach was below the threshold of the receptor.

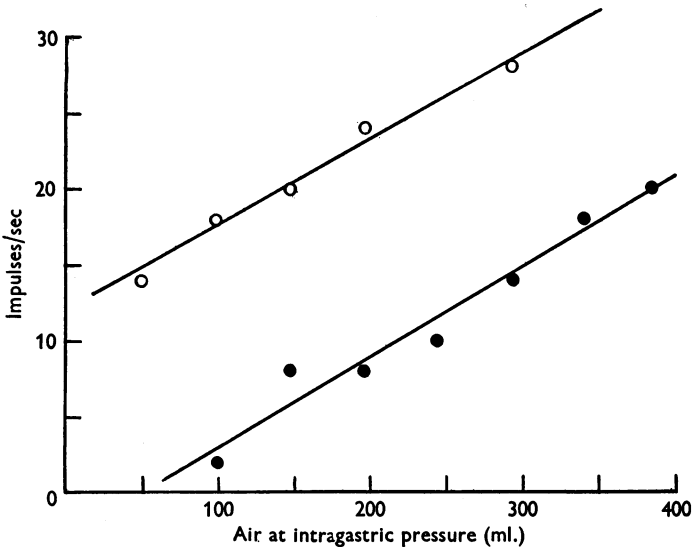


Fig. 9. Relation of degree of distension of the stomach and number of impulses in two gastric stretch afferent fibres from receptors located in the cardiac—●—●— and pyloric—○—○— ends of the stomach respectively.

likely that a rise in intragastric pressure unaccompanied by stretching of the stomach wall does not stimulate the receptors. Apart from the respiratory fluctuation in the discharge seen in one fibre, no other cyclical variations were superimposed on the discharge produced by a maintained distension.

The relation between the degree of distension of the stomach and the frequency of impulses has been determined in five afferent fibres in five different cats. In one, known volumes of air were injected in 20 ml. steps with a 100 ml. syringe such that each succeeding volume was added on to the first. The rate of injection could not be controlled. In two fibres the balloon was distended in 50 ml. steps by a respiration pump each succeeding volume being added on to the earlier one as before. Each inflation was completed in 0.9 sec and the average frequency of impulses over 0.5 sec of the record at the end of the inflation was determined. The volumes of air injected at ambient temperature and pressure were converted into volumes at the corresponding intra-gastric pressures thus giving the actual change in volume undergone by the

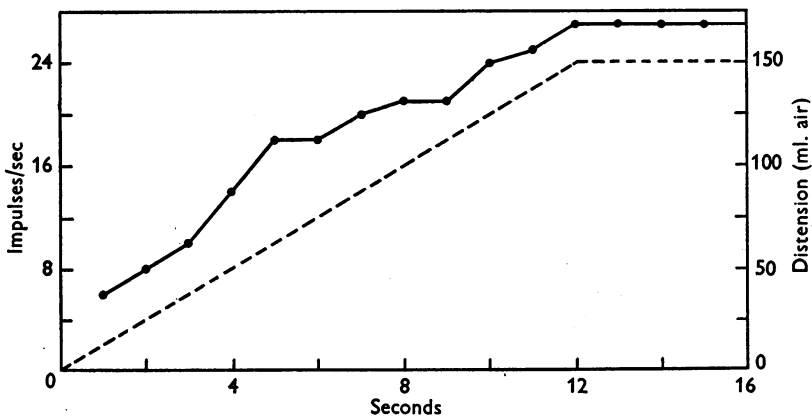


Fig. 10. Frequency of discharge in a gastric afferent fibre with gradual distension of the stomach. The gastric balloon was distended with 150 ml. air in 12 sec as shown by the interrupted line.

stomach. No allowance for temperature was made as there was usually little difference between the environmental temperature (30° C) and the temperature of the stomach which was often exposed to the air through the abdominal wound. As shown in Fig. 9 the relation between the frequency of discharge and degree of distension of the stomach is clearly linear.

Since it was thought that the rate of distension might play an important part in modifying the relationship, each inflation was completed in 0.1 sec in the case of the fourth fibre. Inflations, increasing in 50 ml. steps, were applied and the balloon was completely deflated before the subsequent volume was pumped in. Plotting the peak frequency or the frequency 2 sec after the inflation against the inflating volume again revealed the linear relationship.

As the entry of food into the stomach is a gradual process, it was worth determining whether a gradually increasing distension could be satisfactorily indicated by the receptors. This was done in the fifth fibre (Fig. 10); it is clear that the frequency of discharge follows closely the gradually increasing dis-

tension. In another fibre, distension of the balloon with 200 ml. of water in the course of 2 min resulted in a frequency of discharge identical with that following distension with air.

Conduction velocities

As the conduction velocities of some fibres with receptors sensitive to phenyl diguanide had been determined earlier (Paintal, 1953*b*), the determination of the conduction velocities of gastric stretch afferent fibres was not specially attempted in this investigation, for it has been shown that the great majority of receptors sensitive to phenyl diguanide are located in the stomach (Paintal, 1954*a*). However, the conduction velocity of one fibre was found to be 13 m/sec. In another strand which apparently consisted exclusively of several

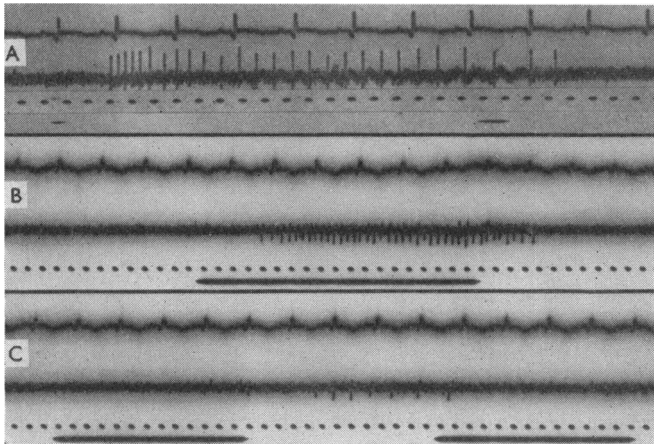


Fig. 11. Localization of gastric stretch receptors. From above downwards in each record, e.c.g.; impulses in a gastric afferent fibre; time in $\frac{1}{10}$ sec; and signal. In A, the cardiac end of the stomach was compressed digitally between the beginning and end of the signal. Records B and C which are from the same fibre show effect of compressing two halves respectively of the partially divided pylorus. In B the pylorus was compressed lightly near the lesser curvature. In C which is from the same fibre as B the pylorus was compressed half an inch away near the greater curvature; note absence of impulses during compression. Records B and C, illustrate degree of accuracy of localization.

gastric stretch afferent fibres, the conduction velocity of the compound action obtained by maximal stimulation of the cervical vagal trunk ranged from 6.5 to 13 m/sec at 38° C. These determinations raise the upper limit of the conduction velocities of fibres with receptors stimulated by phenyl diguanide from 9 to 13 m/sec. The mean conduction velocity of gastric stretch fibres would be about 9 m/sec.

Location of receptors in the stomach

Most of the receptors studied have been localized in the stomach by noting their responses to digital compression or by stretching of the stomach (Fig. 11). The discharge so obtained was always of a higher frequency than could be obtained by mechanical distension of the stomach sometimes reaching about 100 impulses/sec. Although such stimuli are not likely to be encountered in the natural state they were useful in localizing fourteen receptors in different parts of the stomach (Fig. 12). Most of these were localized with certainty within an area of 4 cm², a few within 1 cm². In the case of two out of the four located at the cardiac end of the stomach, removal of the greater part of the stomach left unaffected the responses of the receptors to digital manipulation of the remaining strips of the stomach wall.

Seven receptors were localized at the pyloric portion of the stomach, four near the lesser curvature at the cardiac end, three in the body and one on the greater curvature nearer the pyloric than the cardiac end of the stomach. No attempt was made to determine whether the receptors were situated in the ventral or the dorsal walls of the stomach, but it is believed that they are present in both. The absence or relative infrequency of receptors in the fundus and the major part of the body and greater curvature of the stomach may be significant.

Stroking the mucous membrane or the peritoneal surface of the stomach did not yield a response suggesting that the receptors are probably not located near either of these surfaces but in the smooth muscle itself.

DISCUSSION

It has been shown that there are in the stomach stretch receptors whose response is related to the degree of distension of the stomach and which are probably situated in the smooth muscles of the stomach. It is possible that their disposition in the stomach (Fig. 12), if confirmed, might bear some relation to the tension exerted by the gastric contents on different parts of the stomach. Histological evidence of spindle-shaped receptors in the smooth muscle of the stomach has been provided by Langworthy & Ortega (1943). They are not likely to be situated in or near blood vessels, since superimposed cardiac rhythms have not been observed. The receptors are connected to medullated A fibres, as is obvious from the nature of their spike potentials and conduction velocities. Edgeworth (1892) described such medullated fibres, an observation confirmed by Langley (1892). The fibres concerned probably belong to the smaller group with diameters 1.8–3.6 μ .

The isolation of single units of gastric stretch afferent fibres is more difficult, for several reasons. The fibres are of small diameter and are, therefore, more easily destroyed during dissection; if they are alive their activity is usually

overshadowed by the much greater activity of pulmonary and cardiovascular fibres; they are less numerous, and finally many of them are under the conditions of these experiments inactive in cats starved before an experiment. It is, therefore, not surprising that these receptors have so far remained undetected by various investigators working on the afferent fibres of the vagus. The isolation of these fibres has now been rendered less difficult. By keeping a balloon partially distended in the stomach, fibres showing persistent discharges can be sorted out and can then be identified easily by the methods described.

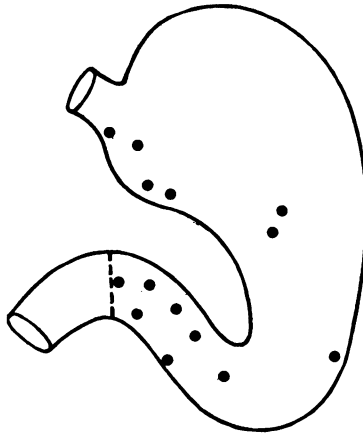


Fig. 12. Location of gastric stretch receptors in the stomach.

There would seem to be little doubt that the normal function of these afferent fibres is to signal the state of distension of the stomach. It is, therefore, apparent that at meal-times or after intake of water large numbers of these impulses would be excited, their number increasing with the course of food or water intake. Maximal stimulation would be achieved when the stomach was fully distended. Thereafter, the number of impulses would continue to reach the brain at a fairly constant rate diminishing but little, since the receptors are very slowly adapting, till the stomach began to empty. The number of impulses would then gradually decrease until the stomach was fully emptied when about a third of the receptors would still be active discharging spontaneously at about 1–10 impulses/sec. When water was drunk, maximal stimulation would presumably be attained earlier and would also cease earlier.

It is suggested that aside from their possible role in various reflexes, such as the gastro-colic, the gastric receptors demonstrated in these experiments are responsible for the immediate feeling of satiation of hunger and thirst which increases with the progress of a meal or intake of water. When the number of

impulses reaches a certain level, feeding or intake of water comes to an end. They probably play little, if any, part in the more permanent satiation that follows absorption of food or water. There is a considerable amount of evidence in support of this hypothesis. The careful experiments of Grossman and co-workers (Janowitz & Grossman, 1949; Share *et al.* 1952) have shown that sham feeding by oesophagostomized dogs depends on the mechanical distension of the stomach whether the distension is achieved by a balloon or calorically inert material. It is bulk rather than caloric content that limits further food intake, and inhibition continues for prolonged periods so long as the distension is present (Share *et al.* 1952). Of considerable interest and one that lends much support to the present hypothesis is the observation by Towbin (1949), that sham drinking in dogs is inhibited by distension of the stomach with a balloon. This response is abolished by vagotomy indicating clearly that the reflex pathway lies in the vagus. Undoubtedly, an efficient mechanism for achieving this exists in the gastric stretch receptors and their vagal afferent fibres. As suggested by the results of Towbin (1949), this afferent mechanism would be responsible only for the immediate temporary satiation of thirst and not the subsequent permanent satiation which follows the intestinal absorption of water.

It is likely that the gastric stretch afferent fibres eventually make connexions with the hypothalamic nuclei which undoubtedly exert a regulatory function on food intake (Brobeck, 1946). The inhibitory influence of the ventromedial nucleus or some neighbouring structure on the so-called 'feeding centre' has been suggested by Anand & Brobeck (1951). If the gastric stretch fibres terminate in the ventromedial nucleus then a reflex mechanism is conceived for the regulation of food intake. Distension of the stomach by food or water would lead to a large number of impulses arriving at the ventromedial nucleus which by stimulating it would lead to inhibition of the feeding centre. The ventromedial nucleus could then be regarded as the satiation centre being largely sensory in function as conceived by Pavlov in his 'food' centre (1928).

SUMMARY

1. The responses of vagal afferent fibres arising from receptors in the stomach were studied in anaesthetized cats. It was shown that a slowly adapting discharge of impulses appears in them following distension of the stomach with a balloon. The endings concerned are, therefore, similar to other stretch receptors in skeletal muscles and the lungs.
2. A linear relation was observed between the degree of distension of the stomach and the number of impulses/sec in the fibres.
3. Some of the fibres showed spontaneous activity in the form of single irregular impulses or groups of impulses; no uniform pattern of activity was found. Most of the fibres were, however, normally inactive when the stomach

was empty and were, therefore, difficult to isolate. Methods have been described to facilitate isolation of these fibres and identify them unequivocally.

4. The conduction velocities of some of the fibres ranged from 6 to 14 m/sec.

5. Fourteen gastric stretch receptors were localized digitally in different parts of the stomach. Most of these were in the pyloric portion of the stomach.

6. It is suggested that the normal function of the gastric stretch fibres is to signal the degree of distension of the stomach and it is believed that they constitute the peripheral mechanism for the immediate satiation of hunger and thirst.

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