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VAGAL MECHANORECEPTORS LOCATED IN THE LOWER OESOPHAGEAL SPHINCTER OF THE CAT

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SUMMARY

1. In anaesthetized cats, sixty-two vagal sensory units with afferent endings in the lower oesophageal sphincter were recorded by means of extracellular glass micro-electrodes implanted in the nodose ganglion.

2. All the receptors had non-medullated fibres, with conduction velocities ranging from 0·8 to 1·2 m/s. From the direct stimulation of the lower oesophageal sphincter, three types of mechanoreceptors were identified.

3. Thirty-one were activated by natural stimuli: tonic contraction of the sphincter and distension elicited by the passage of a bolus. Artificial stimulation effected by digital compression was also effective. These receptors were similar to muscular endings already described in the digestive tract. Their main characteristic, i.e. their slow adaptation, suggests that they act as sensors of sphincter opening and closure. This was corroborated by observations obtained during distension of the cervical or thoracic oesophagus; a maximum decrease occurred in the lower oesophageal sphincter mechanoreceptor discharge when the distension was produced between 9 and 12 cm from the lower oesophageal sphincter.

4. Twenty-nine endings were found in the superficial layers (mucosae). Contrary to the muscular receptors, the mucosal receptors were not affected by normal contractions or distensions of the lower oesophageal sphincter. They were activated only by strong stimuli like digital compression or distension achieved with a balloon. In addition, mucosal stroking was a potent stimulus. Whatever the stimulus used, the mucosal receptors showed rather rapidly adapting discharges. These receptors should be considered to be sensors of bolus consistency.

5. Two mechanoreceptors, located in the serous membrane of the lower oesophageal sphincter, were identified by touching or by stretching. Their discharges showed that they belonged to the rapidly adapting type.

6. A comparison of the three types of receptors found in the lower oesophageal sphincter is made with known digestive endings and their possible role is discussed.

INTRODUCTION

Recent electrophysiological investigations performed in different species have proved the presence of numerous mechanoreceptors throughout the whole digestive

tract, i.e. in the oesophagus (Andrew, 1957; Mei, 1965, 1970*b*; Clarke & Davison, 1975), the stomach (Paintal, 1954; Iggo, 1955, 1957*a*; Leek, 1969; Mei, 1970*b*; Harding & Leek, 1972*a*; Andrews, Grundy & Scratcherd, 1980; in particular), the small intestine (Paintal, 1957; Iggo, 1957*b*; Davison, 1972; Mei, 1970*b*; Ranieri, Mei & Crousillat, 1973; Morrison, 1973; Floyd, Hick & Morrison, 1976; Clarke & Davison, 1978) and the colon (Mei, 1970*a*, *b*; Clifton, Coggeshall, Vance & Willis, 1976). Some of these receptors are located in the muscular layers and are sensitive to normal distensions or contractions affecting the viscera. The others, scattered in the superficial layers (mucosae or submucosae) or in the serous membrane, do not usually respond to these stimuli, unless they are very strong. However, they are able to detect more specific stimuli such as gentle stroking of the mucosae. The physiological role of these receptors is believed to be to provide information on bolus consistency and a large majority are vagal in origin (see Paintal, 1973; Leek, 1977; Mei, 1981). The other endings situated in the stomach or in the duodeno-jejunum, are connected to splanchnic fibres (Ranieri *et al.* 1973; Ranieri, Crousillat & Mei, 1975; Morrison, 1973; Floyd *et al.* 1976). On the contrary, the serosal mechanoreceptors described in the peritoneum (Bessou & Perl, 1966; Ranieri *et al.* 1975; Morrison, 1973; Floyd *et al.* 1976) are only supplied with splanchnic fibres. These serosal mechanoreceptors are stimulated by stretching the whole digestive tract. By contrast, little data is available so far on the lower oesophageal sphincter, which plays an important role in digestion and which presents histological characteristics.

The present work was undertaken to study the whole vagal mechanical sensitivity of the lower oesophageal sphincter, i.e. the muscular, the superficial (mucosal or/and submucosal) and serosal mechanoreceptors. It is based on the micro-electrode technique applied to the nodose ganglia in anaesthetized cats (see Mei, 1970*a*). Preliminary results have been published recently (Clerc & Mei, 1981).

METHODS

Experiments were conducted on thirty-two cats, anaesthetized with Nesdonal (sodium thiopentone, 15 mg/kg) given intravenously, after induction with halothane.

Surgical preparation

The lower oesophageal sphincter area was reached through a median incision which involved either the inferior thoracic region or both the inferior thoracic and superior abdominal regions. The incision was followed by dissection of the diaphragm, around the gastro-oesophageal junction. The chest opening necessitated the use of artificial ventilation adjusted in order to maintain end-tidal CO_2 at 4%. Additionally, the state of the animal was routinely controlled by monitoring the heart rate with an EKG pre-amplifier and by visual observation of the pupil. Finally, in some experiments, the blood glucose level, which is a good physiological index (see Mei, Arlhac & Boyer, 1981), was estimated from time to time with the glucose oxidase method. For this purpose, samples of 100 μl of carotid blood were taken.

The nodose ganglion, usually the one on the right, was dissected under an operating microscope; it was set on a special support to avoid movements due to carotid pulsation and respiratory activity.

Action potential recordings

The unitary activity of sensory vagal neurons was recorded in the nodose ganglion by means of extracellular glass micro-electrodes (Fig. 1). The electrodes, filled with 3 M-KCl solution, were implanted in the latero-external median area of the nodose ganglion which contains most of the cells innervating the lower oesophageal sphincter (see Mei, 1970*b*). Nervous activities were recorded conventionally.

Electrical activation of the vagal nerve

The ipsilateral vagal nerve, with regard to the relevant ganglion, was dissected at the lower cervical level and placed on two silver wires. Electrical stimulation was effected using a stimulator equipped with an isolation unit (type: Grass S88); either single (1 ms; 10–40 V) or repetitive (0·5 ms; 10 V; 2–10 Hz; during 2–10 s) stimuli were used. Thus it was possible to modify the mechanical activity of the lower oesophageal sphincter and to measure the conduction velocity of each neurone studied.

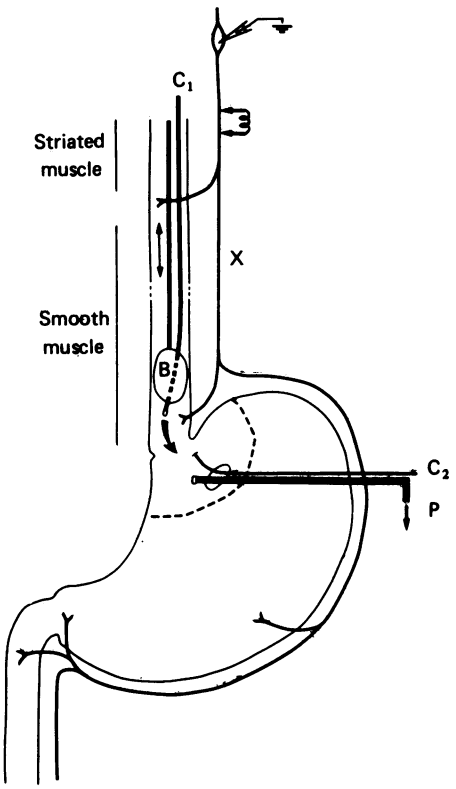

Fig. 1. Experimental procedure used to study the vagal sensory innervation of the lower oesophageal sphincter. C_1, catheter used to perfuse the lower oesophageal sphincter; B, balloon which can be moved by the experimenter (arrow); C_2, catheter used to stroke the mucosae; P, catheter to aspiration pump; X, vagus nerve. The dotted line indicates the position of ligature.

Mechanical stimulation

A balloon was introduced through the mouth and inflated with 5 ml of air. It was either maintained at the same place for 20–40 s or moved within the oesophagus, including the lower oesophageal sphincter.

With one open-tip catheter introduced through the mouth (tip located 3 cm above the lower oesophageal sphincter), it was possible to perfuse the sphincter which was isolated from the gastric fundus by means of a ligature. A second catheter was introduced through a short incision of the fundus, allowing the sphincteric mucosae to be stroked.

Digital compressions were also performed on the lower oesophageal area.

Pressure recording

The open-tip oesophageal catheter or the balloon were conected to a pressure transducer (Telco type). Pressures were recorded on the oscillograph or U.V. recorder along with the vagal action potentials.

RESULTS

In this work, sixty-two mechanoreceptors located in the lower oesophageal sphincter were studied: thirty-one were of muscular origin and thirty-one of non-muscular origin. They were connected to non-medullated vagal fibres. Their conduction velocities ranged from 0·8 to 1·2 m/s (mean: 1·1 ± 0·1 S.E. of the mean).

Muscular mechanoreceptors

Among the thirty-one receptors studied, twenty showed a resting discharge that was either regular (eighteen receptors: discharge frequency, 1–25 impulses/s; mean, 10 impulses/s ± 2·0 S.E. of the mean) or irregular.

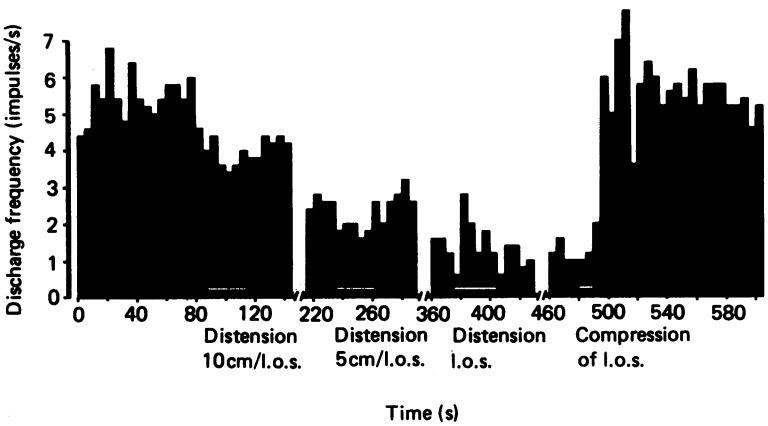

Fig. 2. Effect of oesophageal distension and digital compression on the activity of a spontaneously active muscular mechanoreceptor of the lower oesophageal sphincter. When distensions were performed at 10 and 5 cm from the sphincter (l.o.s.), the discharge frequency always decreased regardless of control firing frequencies. On the contrary, the l.o.s. distension elicited a slight increase in discharge frequency. Bars indicate the duration of distension. In the last histogram, the digital compression of l.o.s. (bar) caused a marked increase of discharge. Note that the regular decrease in control discharge is due to the repetition of stimulations, some of which were performed during interruptions.

Distending the lower oesophageal sphincter by the balloon produced changes in activity of the lower oseophageal sphincter muscular receptors. If the balloon was kept at the sphincteric level, its distension stimulated the silent receptors and increased (36 % on average, l.o.s. in Fig. 2) or decreased (47 % on average) the mean frequency of discharge of the other receptors according to their low (0·8–5·0 impulses/s) or high (above to 5·0 impulses/s) resting discharge frequency respectively. If the balloon was propelled by peristaltic activity or displaced by the experimenter, we observed a transient activation. Stretching the lower oesophageal sphincter also produced activation of receptors.

Digital compression generally had little effect, i.e. a slight activation of receptors discharging at a low rate (Fig. 2). But in the case of highly active receptors, a marked decrease and even a complete arrest of the spontaneous discharge could be observed (Fig. 3*A*).

During the recording of the resting discharge of eight receptors, distension with

variable volumes (3–5 ml) of air was performed along the oesophagus. Various effects were noted according to the location of the balloon. When the distension was produced within a region 5–12 cm from the sphincter, i.e. within the thoracic oesophagus and the last part of the cervical oesophagus, the on-going discharges were always decreased regardless of control firing frequencies. The maximum effect was obtained 9–12 cm from the lower oesophageal sphincter as illustrated in Fig. 4

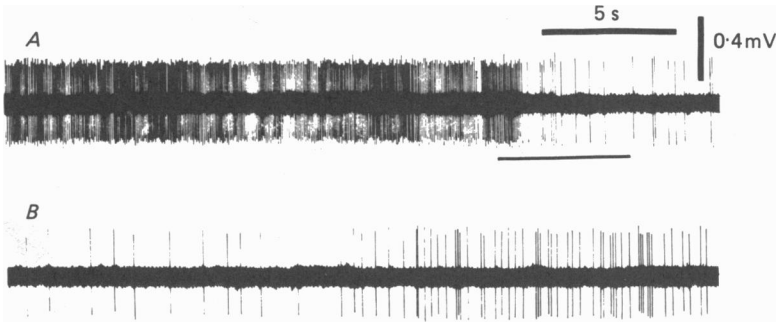

Fig. 3. Muscular mechanoreceptor located in the lower oesophageal sphincter exhibiting a high sustained resting discharge. *A*, the digital compression of the sphincter (line below the action potential recording) caused a marked decrease in spontaneous discharge; *B*, this effect lasted some seconds, but at the end of *B*, the discharge frequency tended to recover. *A* and *B* are continuous recordings.

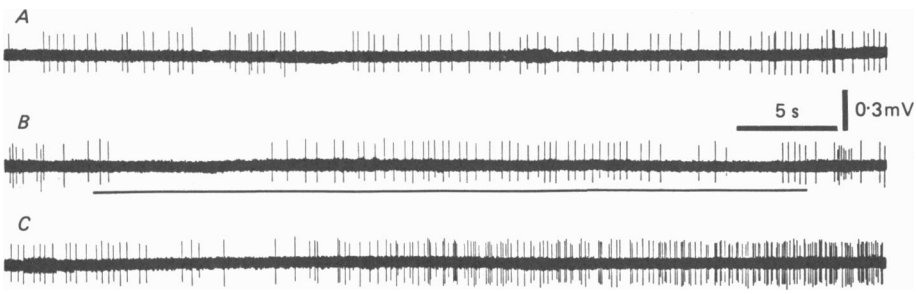

Fig. 4. Muscular mechanoreceptor situated in the lower oesophageal sphincter. Change of its resting discharge due to distension of the striated oesophagus. *A*, resting activity; *B*, distension of the oesophagus at 11 cm from the sphincter (line); the discharge completely disappeared during about 8 s; *C*, the discharge is higher than in control, probably because of the sphincteric phasic closure. *A*, *B* and *C* are continuous recordings.

where the control activity was completely silenced with a slow and progressive recovery. When the distension was performed close to the lower oesophageal sphincter (0–5 cm), we observed either a decrease or an increase in the basal activity (Fig. 2).

Short, repetitive, electrical stimulation of the cervical vagal nerve (2–4 s) produced a reinforcement of the lower oesophageal sphincter closure. In this circumstance the resting discharge of twelve mechanoreceptors was enhanced (mean frequency: from $2{\cdot}6 \pm 1{\cdot}1$ to $10{\cdot}1 \pm 2{\cdot}9$ impulses/s) (Fig. 5*B* and *C*; Fig. 6*B*) and three receptors, previously silent, were caused to discharge.

Such stimulation might also elicit a decrease in discharge, especially after several repetitive tests. In Fig. 6, we can observe that the effect of electrical stimulation of the vagal nerve is shown to depend on the degree of contraction of the lower oesophageal sphincter (which is indicated by the change in discharge frequency of the receptor). In this example, the last stimulus (St. 4), unlike the previous stimuli (St. 1, St. 2, St. 3) enhances the activity of the receptor.

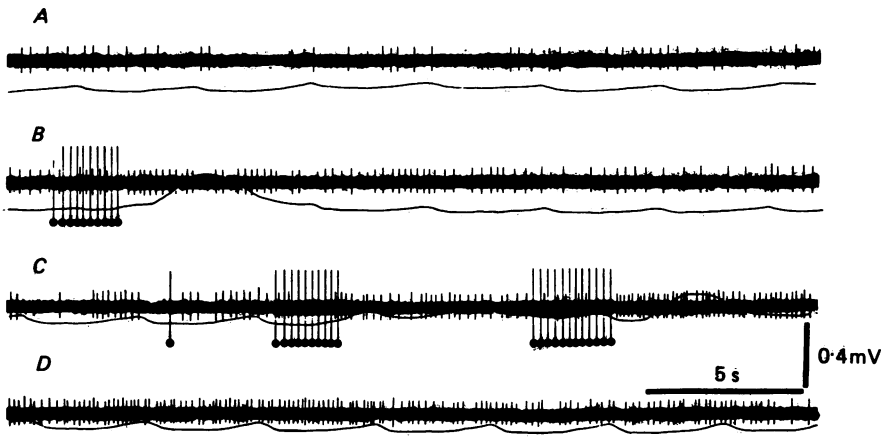

Fig. 5. Effect of the vagal electrical stimulation on the activity of a muscular mechanoreceptor located in the lower oesophageal sphincter. *A*, resting activity recorded together with the endoluminal pressure; *B*, after repetitive stimulation (0·5 ms; 10V; 4/s), a contraction occurred; the discharge was enhanced (dots below: stimuli artifacts); *C* and *D*, this effect was more marked after a single and two repetitive stimulations. *A* and *B* on the one hand, and *C* and *D* on the other hand, are continuous recordings.

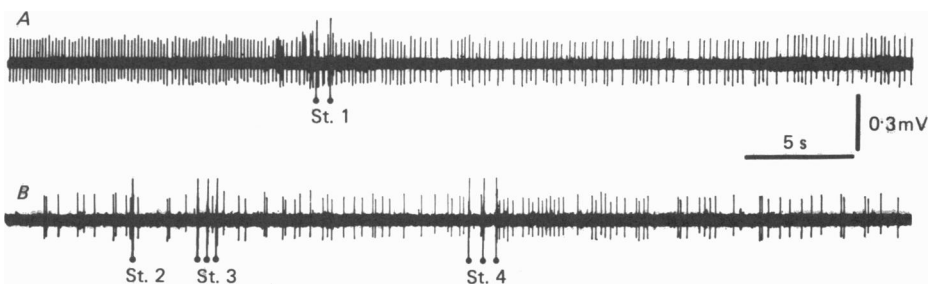

Fig. 6. Effect of the vagal electrical stimulation on the activity of a muscular mechanoreceptor of the lower oesophageal sphincter. *A*, after two electrical stimulations (St. 1 = 0·5 ms; 10 V), the spontaneous activity decreased; *B*, after St. 2, the phenomenon is still marked. In return, St. 3 and chiefly St. 4 caused an enhancement of the discharge frequency.

Non-muscular mechanoreceptors

Mucosal mechanoreceptors. Among the twenty-nine receptors studied in the lower oesophageal region, only two exhibited a resting activity: one discharged regularly at a low frequency (1 impulse/s), the other presented irregular bursts (mean: 3 impulses/s).

Moderate distension of the sphincteric area did not cause the activation of non-muscular receptors. Contractions induced by electrical stimulation of the vagal

nerve did not elicit responses in those receptors, except in six cases for which a late and direct activation occurred (Fig. 7), with no relation to variations in intraluminal pressure. Strong and rapid distension could excite the lower oesophageal sphincter

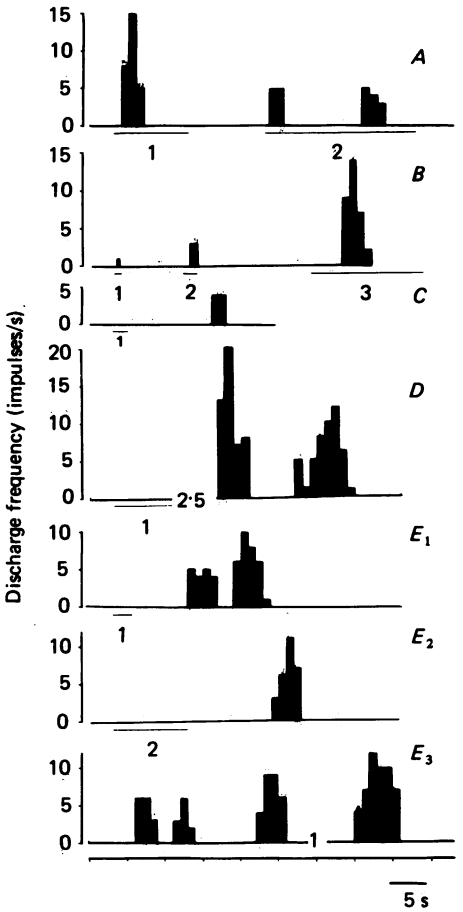

Fig. 7. Histogram representation of a mucosal mechanoreceptor. *A*, responses elicited by two strong distensions (1 and 2); *B*, responses due to strong digital compression (1, 2 and 3); *C*, late response caused by electrical stimulation of vagus nerve (1); *D*, discharges occurred later, after HCl solution (pH 2) (1). E_1, response to saline solution, rapidly administered; E_2, response to saline solution, slowly administered; the latency is longer; E_3, responses occurred, although no further stimulation was performed. E_1, E_2 and E_3 are continuous traces. 2·5 and 1 express the duration (in min) of recording interruption in *D* and E_3 respectively.

mucosal mechanoreceptors (Fig. 7). These mucosal mechanoreceptors located in the lower oesophageal sphincter were also activated by digital compressions (Fig. 8). There was however no systematic relationship between discharge and stimulation.

Responses of sphincteric mucosal mechanoreceptors were regularly evoked by mucosal stroking (Fig. 8), and they were also activated by strong and rapid injections of saline solution. However, warm perfusions with saline solutions at temperatures below 50 °C had no effects; at temperatures ranging between 50–52 °C, one receptor

only was activated (Fig. 8). Chemical tests (HCl solution, pH 2; glucose solution 100 g/l, i.e. 550 mosmol/l) were used for four receptors; only one receptor was activated by HCl and none by glucose.

Serosal mechanoreceptors. The two serosal mechanoreceptors studied were initially silent. They were activated by stretching and stroking the serous membrane at

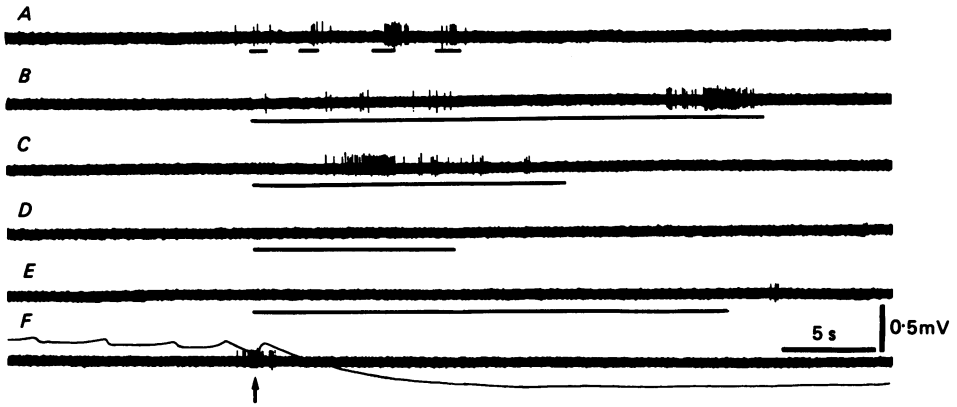

Fig. 8. Mucosal mechanoreceptor. *A*, digital compression of the lower oesophageal sphincter; *B*, stroking of mucosae with a polyethylene catheter; *C*, perfusion with a warm solution of water (50 °C); in all the cases, responses were elicited. However, in *D*, perfusion with water at 37 °C had no effect and in *E*, HCl (pH 2) did not cause a concomitant response with stimulation; nevertheless, three spikes occurred after the end of stimulation. *F*, the distension with a balloon displaced from thoracic oesophagus to stomach produced a response (arrow). Lines indicated the duration of stimulations.

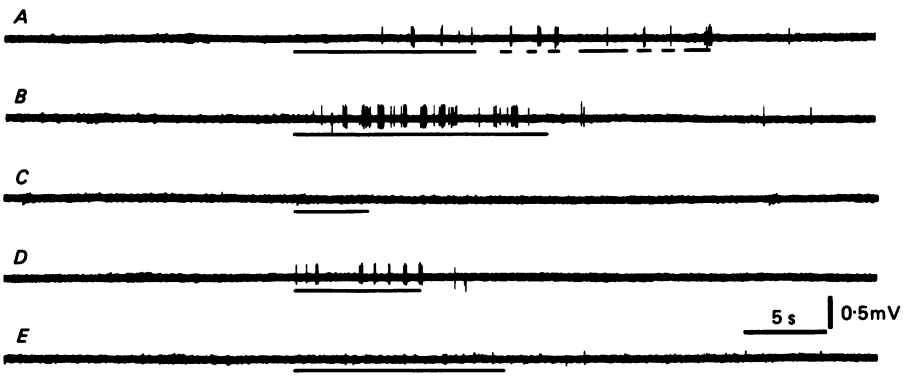

Fig. 9. Serosal mechanoreceptor situated in the lower oesophageal sphincter; effects of mechanical stimuli performed at this level. *A*, responses to digital compressions; *B*, response to stretching; *C*, distension with a balloon had no effect; *D*, 1 min after local application of xylocaine, the response was diminished in comparison with *A*; *E*, 1 min later, no response occurred after this stimulation. Lines indicate the duration of stimulations.

sphincteric level or by compressing the whole lower oesophageal sphincter (Fig. 9). One reacted to hot air at 50 °C blown onto the serous membrane. Other forms of stimulation which were able to activate the muscular and mucosal mechanoreceptors were ineffective (contraction and liquid passage in particular). The application of xylocaine to the serous membrane at the sphincter level suppressed the responses to stretching, stroking and compression (Fig. 9).

DISCUSSION

Thanks to the micro-electrode technique, it has been possible to systematically study the mechanical sensitivity of the lower oesophageal sphincter in anaesthetized cats. Three types of mechanoreceptors have been identified according to their location and their functional characteristics: the muscular, the mucosal and the serosal mechanoreceptors. So far the latter two have not been described in this part of the digestive system.

Muscular mechanoreceptors

The muscular mechanoreceptors, like the other digestive muscular mechanoreceptors, are activated by both contraction and distension. Nevertheless, at this level, contraction seems much more efficient than distension, perhaps because the effect of artificial distension is reduced by the normal tonic contraction of the sphincter (resting-closure). Their slowly adapting response as well as their low threshold suggest that these mechanoreceptors act as sensors of sphincter opening and closure. Therefore they may promote the reflex maintenance of tone during resting-closure and also during the phasic closure which follows the passage of a bolus (see Miolan & Roman, 1978).

Because of their functional characteristics, the muscular mechanoreceptors give precise information on the mechanical state of the sphincter. Consequently, it has been proposed to use their discharge recording to analyse the mechanical variations occurring at this level (Mei, Salducci, Monges & Farnarier, 1972; Falempin, Mei & Rousseau, 1978). In the present work, we have developed this technique in order to investigate the effects of oesophageal afferents on the lower oesophageal sphincter activity. The discharge decrease of sphincteric mechanoreceptors resulted probably from activation of the oesophageal muscular mechanoreceptors during maintenance of distension and the occurrence of extrinsic regulation. This phenomenon reached a maximum when distension was evoked 9–12 cm from the sphincter. This is certainly related to the strong concentration of mechanoreceptors in this region (Mei, 1965, 1970*b*; Falempin, 1981). The decrease in sphincteric receptor activity noted when distension was achieved in lower oesophagus (less than 9 cm from the sphincter) might be differently interpreted. In this area, only constituted with smooth muscle, the muscular mechanoreceptors might act through intrinsic reflexes which are predominant in the smooth oesophagus (Roman & Tieffenbach, 1971; Tieffenbach & Roman, 1972).

Mucosal mechanoreceptors

The mucosal mechanoreceptors found in the lower oesophageal sphincter region are similar to those already described in the gastro-intestinal tract (Paintal, 1957; Iggo, 1957*b*; Mei, 1970*b*; Andrews & Andrews, 1971; Harding & Leek, 1972*b*). They are characterized by the following features: (1) usually, they are silent, unlike the muscular mechanoreceptors of the lower oesophageal sphincter, (2) they are easily activated by mucosal stroking which represents a potent stimulus, (3) they also respond to other stimuli, such as strong distension and digital compression, but the responses elicited are not simply related to stimulation since they continue to discharge after stimulation ends, (4) generally the responses produced by these

various stimuli adapt rapidly and (5) most of them seem to be sensitive only to mechanical stimulation (specific mechanoreceptors), whereas the others respond to any stimulus and thus constitute a different class of endings (non-specific or polymodal receptors).

The number of mucosal mechanoreceptors is higher than in other parts of the digestive tract, possibly because the muscularis mucosae displays a greater development in the lower oesophageal sphincter than in the other parts of the gastro-oesophageal tract. At this level, the muscularis mucosae presents a maximum thickening and is organized into numerous bundles, in man (Giordano-Lanza & Manieri, 1961; De Carvalho, 1971), in rabbits (Cecio, 1976), and in cats (N. Clerc, unpublished observations).

From their functional characteristics, we can suggest three possible roles for mucosal mechanoreceptors. First, to inform the C.N.S. as to the quality of nutriments in contrast to the muscular mechanoreceptors which give information on the state of the organ. This may indicate that they act as texture sensors (Paintal, 1957; Leek, 1977). Secondly, they may intervene with the muscular mechanoreceptors to initiate the phasic closure of the sphincter after passage of a bolus. Thirdly, they may be involved in pathological conditions as a consequence of the powerful contractions of muscularis mucosae to the marked stretching and distension which occur during vomiting.

Serosal mechanoreceptors

The serosal mechanoreceptors studied in the lower oesophageal sphincter belong to the rapidly adapting type and their stimulation threshold seems high. Therefore, their potent stimulus might be the strong stretching and distension which occur in special circumstances such as vomiting. Although the vagal nerves do not supply the serous membrane of the digestive tract in general (see McSwinney & Suffolk, 1938; Mei, 1970*b*), it is demonstrated here that a few serosal vagal mechanoreceptors are scattered in the lower oesophageal sphincter.

Finally, the present report confirms the general complexity of the digestive mechanical sensitivity revealed by electrophysiological investigation (see Mei, 1970*b*, 1978; Paintal, 1973; Leek, 1977).

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