CENTRAL NERVOUS CONTROL OF GASTRIC MOVEMENTS IN SHEEP AND GOATS

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The co-ordinated periodic gastric movements in ruminants can be abolished by bilateral vagotomy (Mangold & Klein, 1927; Popow, Kudrjavcew & Krasausky, 1933; Duncan, 1953) which cuts both the gastric motor fibres and gastric sensory fibres. The gastric motor fibres in the vagi were first described by Hartung (1858), whereas it is only recently that vagal afferent fibres with reflex effects on ruminant gastric motility were described (Duncan & Phillipson, 1951; Duncan, 1952). Titchen (1953, 1954) independently observed these reflex effects and showed that moderate gastric distension or increased acidity of the abomasal contents reflexly enhanced gastric motility.

The present investigations were started in order to analyse the afferent and efferent reflex pathways. Gastric afferent receptors have been identified electrophysiologically (Iggo, 1955) and an attempt has been made to see how far these receptors may be responsible for the reflexes observed. Some of the results have already been described briefly (Iggo, 1951).

METHODS

Sheep of various ages, weighing 25–45 kg, and male goats, 3–9 months old and weighing 15–35 kg were used. Permanent ruminal cannulae were fitted in all sheep, by the method of Phillipson & Innes (1939), several weeks before the acute experiments were done. In acute experiments the stomach was exposed, if necessary, by an incision in the abdominal wall. The cervical vagus was exposed by a longitudinal skin incision and covered by a pool of liquid paraffin B.P. at 37–39° C, which filled a trough formed by tying the skin flaps to a supporting frame.

Vagotomy above the left nodose ganglion was done in aseptic conditions. A lateral approach was used and the ganglion was located by following the cervical vagus up towards the skull.

For decerebration the animal, starved overnight, was anaesthetized with a single dose (approx. 25 mg/kg) of pentobarbital. After tracheal cannulation the dorsal surface of the cranium was exposed, the common carotid arteries were clamped and an opening was made in the skull with a ¾ in. diameter trephine. The hole was enlarged across the mid-line after the dura mater had been detached from the bone, the longitudinal sinus was ligatured and the dura mater taken off the

exposed cortex. Next the vertebral arteries were compressed manually against the second cervical vertebra and a thin metal spatula, inserted behind the elevated right occipital pole of the cortex, was drawn across the brain-stem in an intercollicular plane. After removing the severed brain the stumps of the internal carotid arteries were clamped and ligated and the stump of the basilar artery was compressed with fibrin foam. The clamps were removed from the common carotid and vertebral arteries after a clot had formed on the basilar artery. This technique has been used on thirty-five sheep and two goats with three deaths at decerebration.

Recording methods. Gastric movements were recorded with air-filled balloons in the stomach connected either to water manometers and a kymograph, or to condenser manometers and an oscillograph.

Electrical activity in single afferent fibres was recorded by a method previously described (Iggo, 1955). The compound action potentials in the right or left cervical vagus, set up by electrical stimulation, were recorded by fixing one Ag/AgCl electrode to the severed end of the nerve and placing the other Ag/AgCl electrode distant 1–2 cm along the nerve. The vagus between the electrodes was crushed (in some experiments a drop of a 1 % (w/v) solution of procaine HCl was also placed on the 'end' electrode) so that monophasic action potentials were recorded. The pair of stimulating electrodes was placed under the vagus 35–90 mm away, and part of the intervening vagus was left attached to the surrounding tissues. The Ag/AgCl earth electrode was stitched into nearby muscle. The action potentials, amplified with a conventional amplifier, were displayed on a cathode-ray screen and recorded on film (Ilford 5B52).

Excitation of gastric afferent or efferent fibres was detected by recording the intragastric pressure while stimulating faradically the central or peripheral end, respectively, of the cut cervical vagus. Single compound action potentials elicited by stimuli of the same intensities were photographed. The conduction velocity of the gastric fibres was measured from the potential wave obtained by subtracting the compound action potentials set up by stimuli subthreshold for gastric movements from those set up by stimuli above threshold.

Histological method. Pieces of the vagi were taken from sheep and goats at or just before death and were fixed in the vapour above a 1 % (w/v) solution of osmic acid. The nerves were embedded in paraffin wax and transverse sections (6μ thickness) cut. The diameters of the myelinated fibres were measured with an eyepiece vernier micrometer and during counting each fibre was pricked off on an enlarged photograph of the section as it was measured on the slide.

RESULTS

When intact sheep and goats were anaesthetized the co-ordinated reticulo-ruminal movements ceased and began again, during recovery from anaesthesia, after fore-limb flexion could be elicited reflexly (Table 1). The returning reticulo-ruminal movements were small, slow and far apart at first and were often

TABLE 1. The effect of anaesthesia, induced by intrajugular single injections of the drugs listed, on reticulo-ruminal motility in sheep

| | | | Time to recovery (min) | | |
Drug	No. of experiments	Dose mg/kg	Flexor reflex in forelimb	Reticulo-ruminal motility	Standing posture
Thiopentone	7	13–25	9–33	10–33	20–76
Pentobarbital	11	17–25	10–22	16–39	60–92
Allobarbitone	3	32–33	Not absent	12–26	115–318
Chloralose	1	40	Not absent	*Absent for 5 min, 30 min after injection	—
Urethane	1	320	Not absent	*Not absent	—

* Decrease in size and frequency of movements.

followed by a series of progressively smaller rhythmic ruminal movements which had died out before the next reticulo-ruminal contraction began.

Reticular movements were also elicited in a lightly anaesthetized goat by sustained reticular or ruminal distension (Table 2, Fig. 3). The response was abolished by giving more pentobarbital.

In a series of eighteen decerebrate sheep typical reticulo-ruminal contractions, at frequencies ranging from 0·5 to 1·0 per minute, were recorded (Fig. 1)
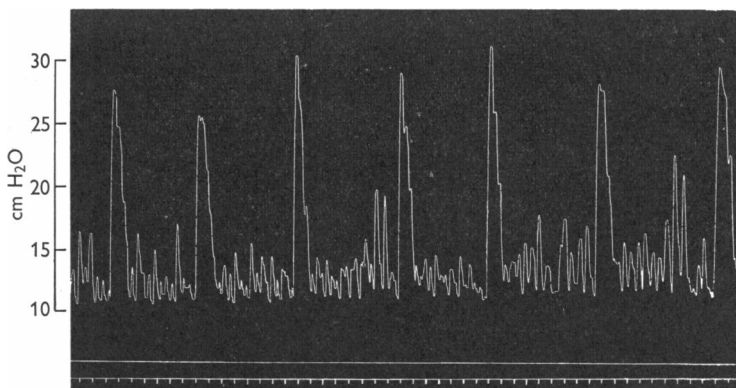

Fig. 1. Large ruminal contractions recorded in a sheep 15 min after decerebration. Reticular contractions recorded several minutes later had the same frequency. Time marks in lowest tracing at 10 sec intervals.
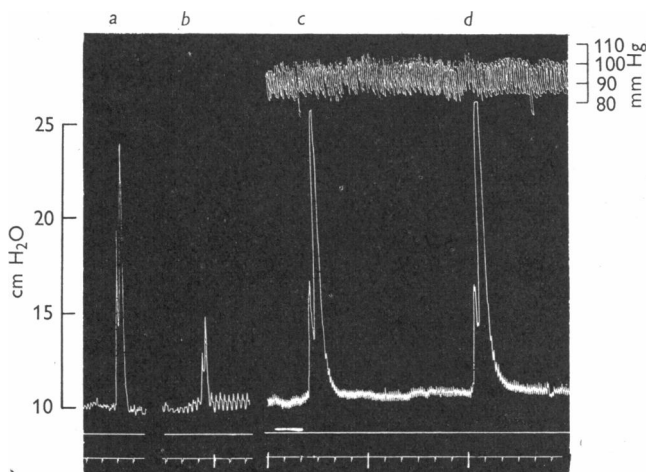

Fig. 2. Diphasic reticular contractions in a sheep. a, in the conscious animal; b, under light pentobarbital anaesthesia; c, a contraction elicited by faradically stimulating the central end of an abomasal nerve 40 min after decerebration followed by d, a spontaneous contraction. The upper tracing in c and d shows the carotid arterial pressure, the middle tracing shows the reticular movements and below are the signal tracing and time marks at 10 sec intervals.

in seven preparations within 15 min of dividing the brain stem. In four preparations, which did not show these spontaneous movements, gastric movements were elicited by brief faradic stimulation, 20–100 c/s for 5–20 sec, of the central cut end of cervical, thoracic or abdominal branches of the vagi. Such stimulation sometimes elicited one diphasic contraction (Fig. 2), and at other times aroused a succession of diphasic movements which continued for as long as 30 min (e.g. Fig. 5). In other decerebrate preparations the interval between successive reticular movements elicited by repeated faradic vagal stimulation was never less than 10 sec. Each burst of stimuli in a series of 10 to 20 elicited a contraction only if the interval between successive bursts was 30 sec or longer.
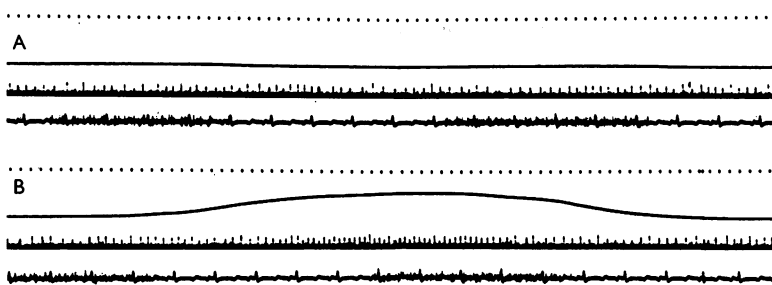

Fig. 3. Impulses in a single vagal afferent fibre during reticular distension and a reticular contraction in a lightly anaesthetized goat. A, the effect of sustained distension (1200 ml.) on the single fibre; B, a reticular contraction elicited by the same distension, which is continuous throughout. In each record the upper tracing shows the intra-reticular pressure, the middle tracing shows impulses in the single afferent fibre and the lower tracing shows the e.c.g. and impulses in an external intercostal muscle. Time $\frac{1}{10}$ sec.

The afferent limb of the gastric motor reflex

Impulses in centripetal vagal fibres from gastric receptors were recorded during reticular, ruminal or abomasal distension in anaesthetized sheep and goats (Fig. 3). Five receptors were found by squeezing small areas of the gastric wall between finger and thumb and were all near the oesophageal groove; these receptors were excited by both reticular and ruminal distension.

During sustained reticular distension in one lightly anaesthetized goat, impulses were recorded in three single afferent fibres and reticular movements were elicited (Fig. 3). Increasing the volume of distension from 800 to 1200 ml. doubled the rate of firing of impulses and decreased the interval between successive reticular contractions (Table 2). In the more deeply anaesthetized animal the same distension no longer caused reticular movements, although the discharge in the single fibres was unchanged.

The conduction velocity was measured in centripetal fibres from tension receptors, where it was 2–12 m/sec, and in those vagal fibres faradic stimulation

of which elicited gastric contractions in decerebrate sheep. The compound action potential method was used for the latter (Fig. 4), and in five preparations the conduction velocity of the most excitable gastric afferent fibres was 10–13 m/sec. When the intensity of stimulation was raised above the threshold for a reflex response the latent period of the gastric movement was less and fibres with conduction velocities less than 10–13 m/sec were excited. The shortened latent period is attributed to an excitatory effect of some of these slower fibres. With this technique it was not possible, however, to assess the conduction velocity of the slowest gastric afferent fibres.

TABLE 2. The effect of the volume of sustained reticular distension on the discharge of impulses in three single vagal afferent fibres and on the interval between reticular contractions elicited by the distension; and the effect of the contractions on the discharge in the single fibres. The contractions were recorded under isometric conditions (Goat)

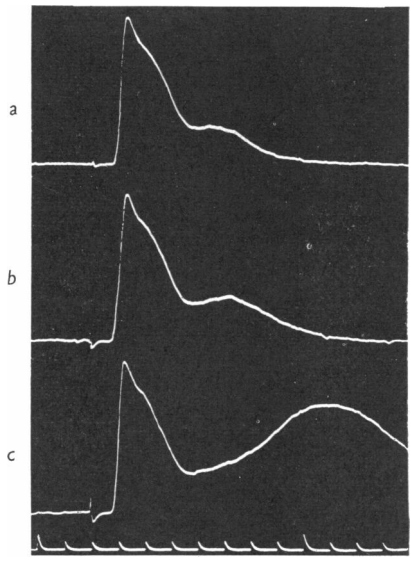| Fibre	Volume of distension (ml.)	Rate of discharge (impulses/sec)		Interval between contractions (sec)
		Distension	Contraction	
a	1200	10–14	48–61	30, 45, 45
b	800	8–11	18–30	—
	1200	15–19	23–46	30, 25, 30, 60 30, 55, 30, 50 50, 50, 55.
c	800	15–22	37–44	70, 60
	1200	37–45	46–63	—

Fig. 4. Compound action potentials, set up by single stimuli, recorded from the central end of the severed cervical vagus in a decerebrate sheep. The stimulus intensity was just subthreshold for excitatory gastric afferent fibres in *a*, just threshold in *b*, and was supramaximal for the myelinated fibres in *c*. Time marks in msec. The conduction distance was 56 mm.

The efferent limb of the gastric motor reflex

A succession of reticulo-ruminal movements in a decerebrate sheep could be broken by blocking both cervical vagi (Fig. 5). When only one vagus was blocked, or if both vagi were partly blocked, the movements were still present but smaller and farther apart than before applying the block. Faradic stimulation (8–100/sec) of the peripheral end of the cut cervical vagus caused smooth
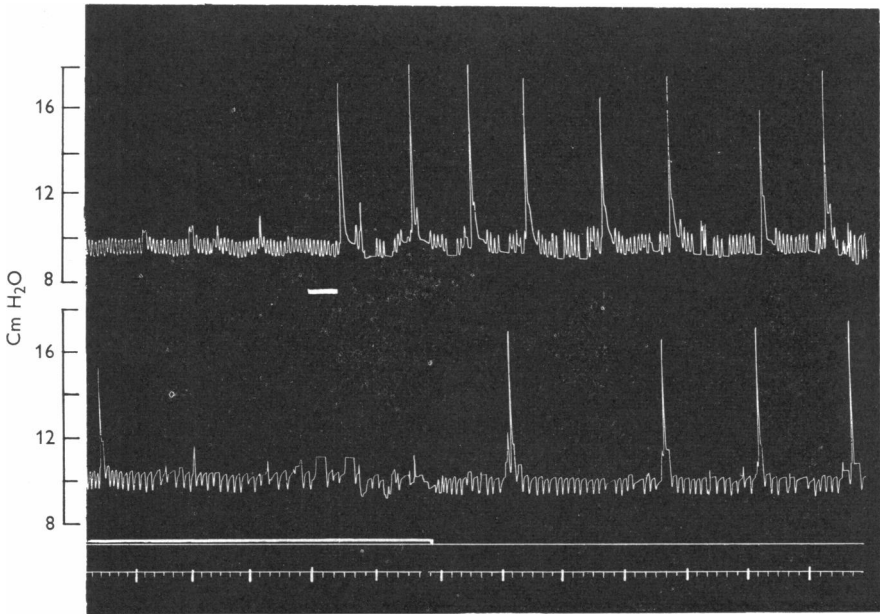

Fig. 5. The effect on a succession of reticular contractions in a decerebrate sheep of cooling both cervical vagi with 4° C saline. The records are continuous and the period of cooling is indicated by the signal in the lower tracing. The contractions were elicited 5 hr after decerebrations by faradic stimulation of an abomasal branch of the vagus for 25 sec shown by the signal below the upper tracing. The balloon was not deep in the reticulum in this experiment. Time marks are at 10 sec intervals.

gastric contractions. The conduction velocity of the most excitable of these gastric efferent fibres, measured by the compound action potential method in four anaesthetized and two decerebrate sheep, was 11–16 m/sec. When the stimulus intensity was above the threshold for gastric contractions slower vagal fibres were excited and the gastric contractions were more powerful. There was no further increase in the strength of the gastric contractions when the stimuli were strong enough to excite the non-myelinated fibres in addition to the myelinated fibres. From these results it is concluded that the gastric efferent fibres in the cervical vagi had conduction velocities of 1–16 m/sec.

The left vagus was cut above the nodose ganglion in three sheep, and at least 40 days were allowed for degeneration of the de-centralized fibres. At the end of that time the vagi were stimulated faradically during acute experiments. No gastric movements were caused when the left vagi were stimulated, but the stomachs were sensitized by the denervation to stimulation of the right vagi.

Myelinated fibres in the abdominal vagi

In cross-section of osmic-acid stained dorsal and ventral abdominal vagi and in ruminal and abomasal branches of the vagi myelinated fibres were abundant. There were several thousand at the diaphragmatic level of the vagus in sheep and goats and in a sample counted in one sheep 80 % were $2-4\mu$ diameter, 14 % were $4-6\cdot5\mu$ diameter and only 3 % were $7-12\mu$ diameter. The largest fibres were absent from cross-sections of abomasal and ruminal nerves, but the size distribution was otherwise similar.

DISCUSSION

The gastric tension receptors behaved in a manner consistent with the view that they mediate the excitatory effect of gastric distension. At volumes of distension adequate to elicit reticular movements impulses were being discharged along the centripetal fibres from the receptors, and the more powerful excitatory effect of a larger volume of distension, also found by Dussardier (1955), was matched by a higher rate of firing in the afferent fibres.

Evidence from the conduction velocity studies is also consistent with this hypothesis. The centripetal fibres from the tension receptors had the same range of conduction velocities, less than 13 m/sec, as vagal afferent fibres with a known excitatory effect on the gastric centre, viz. those afferent fibres which on faradic stimulation elicited gastric movements.

A problem arises, however, because all the gastric receptors so far isolated in single fibre preparations in goat and cat (Iggo, 1955) have behaved as 'in series' tension receptors, i.e. the receptors were excited by both passive distension and active contraction of the stomach. A distension-elicited contraction should, therefore, be self-perpetuating, for the rate of firing in afferent fibres during the contraction would be greater than during the preceding distension and so the excitatory effect of distension would be re-inforced. This, in fact, does not happen, presumably because the gastric centre becomes inexcitable for a time after a reflexly elicited contraction. This was found, for example, when the gastric afferent fibres in the vagi were stimulated electrically in decerebrate sheep and two reticular contractions could not be elicited with less than 10 sec between them.

Afferent fibres in the splanchnic nerves shown by Duncan & Iggo (unpublished observations, 1950) and Titchen (1954) to be inhibitory are not essential to the normal function of the gastric centre since gastric movements were

present in splanchnicotomized sheep (Duncan, 1953). These fibres may mediate the inhibitory effect of abomasal distension (Phillipson, 1939).

The disappearance of reticulo-ruminal movements when the cervical vagi were blocked in decerebrate sheep and their absence in conscious sheep when the vagi were blocked (Popow *et al.* 1933) or cut (Duncan, 1953) is convincing evidence that the gastric efferent fibres are restricted to the vagi. This conclusion is confirmed by Bell & Lawn (1955), who showed that monophasic reticulo-ruminal contractions evoked by electrical stimulation of the dorsal part of the lateral reticular formation in the medulla of sheep were abolished by ipsilateral vagotomy. A centre such as that which Bell & Lawn were stimulating was presumably active during the reflex and spontaneous reticulo-ruminal movements in the decerebrate preparations. However, these latter movements displayed a co-ordination which was lacking when the medulla was stimulated directly, and it is clear that the finer details of gastric centre function have yet to be revealed.

The normal pattern of gastric movements seems to depend on the gastric centre since faradic stimulation of the gastric efferent fibres caused smooth unco-ordinated gastric contractions. Whether the pattern arises in the internal organization of the centre or is, in part, determined by afferent inflow from the stomach is a subject for investigation.

SUMMARY

1. Reticulo-ruminal movements which ceased when intact sheep or goats were anaesthetized could be elicited by gastric distension in a lightly anaesthetized goat. In decerebrate sheep and goats they appeared spontaneously or were elicited by gastric distension or by faradic stimulation of the central end of the cut vagus.

2. Sustained gastric distension elicited reticular movements and excited receptors in the gastric wall. Increasing the distension raised the rate at which impulses were firing in centripetal fibres from the receptors and shortened the interval between successive contractions. The centripetal fibres from the gastric receptors and the vagal afferent fibres, faradic stimulation of which elicited gastric movements, had conduction velocities less than 13 m/sec.

3. A series of reticulo-ruminal movements in decerebrate sheep could be abolished by blocking the cervical vagi. The gastric efferent fibres had conduction velocities of 1–16 m/sec and when they were stimulated repetitively smooth unco-ordinated gastric contractions were recorded.

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