

ON THE ORIGIN, COURSE AND CELL-CONNECTIONS
OF THE VISCERO-MOTOR NERVES OF THE
SMALL INTESTINE. BY J. L. BUNCH, M.D., B.Sc.
(Seventeen Figures in Text.)

(From the *Physiological Laboratory, University College, London.*)

CONTENTS.

Historical.

Method.

Normal movements and effect of drugs.

Influence of various nerves—vagi.

splanchnics.

mesenteric nerves.

The nerve-outflow to the intestine from the spinal cord.

Influence of nerves upon the stomach.

The nerve-cell connections of the intestinal visceromotor nerves.

Historical.

Splanchnic. The influence of the splanchnic on the intestine was investigated by Johannes Müller¹ as long ago as 1837; he found that stimulation of the splanchnic or of the cœliac ganglion caused contraction of the intestine, and that this result was still obtained after section of the vagi. Volkmann² in 1845 showed that excitation of the splanchnic major in a cat caused contraction of the stomach. Ludwig³ in 1853 found that excitation of the splanchnic caused inhibition of the intestinal movements, while section of the splanchnic caused no alteration in the normal rhythm of the intestine.

Pflüger⁴ in a series of experiments between 1855 and 1857 proved that excitation of the dorsal cord inhibited the intestinal movements, but that this inhibition was no longer obtained after section of the

¹ *Handbuch d. Phys. des Menschen*, i. 1837.

² *Müller's Archiv*, 1845.

³ *Lehrbuch d. Phys. des Menschen*, i. p. 179.

⁴ *Ueber das Hemmungs-Nervensystem f. d. peristaltischen Bewegungen d. Gedärme*, 1855, &c.

splanchnics. Stimulation of the peripheral end of the divided splanchnic again caused inhibition, and this inhibition was accompanied by relaxation of the intestine. Comparing this result with that obtained by inhibitory nerves on the heart, he formulated a theory of inhibition, whether cardiac or intestinal, which assumed that inhibitory nerves transform the activity of motor ganglia and suppress it momentarily.

Schiff¹ was the first to oppose Pflüger, for though he admitted the inhibitory action of the splanchnic, he denied that the explanation of its action was correct. The splanchnic, he said, was a motor nerve, and on weak excitation caused movements of the intestine. This was a physiological excitation, but when the nerve was exhausted by too strong a stimulus, its activity was diminished and the pre-existing movements ceased.

Another interpretation of Pflüger's results, and one which could be reconciled with those of Ludwig and Haffter² (1853) and of Ludwig and Kupfer³ (1857), was enunciated by Nasse⁴ (1866), who held that the splanchnic contained both motor and inhibitory fibres. During life the inhibitory fibres are predominant, and on stimulation only inhibition is seen; after death, the excitability of the inhibitory fibres disappears sooner than that of the antagonistic fibres, and stimulation causes movement. The first of these conclusions was generally admitted, but considerable opposition was raised by the second. Ludwig and Kupfer had already stated their opinion that the splanchnic contained both motor and inhibitory fibres, and demonstrated the former action in the cat, the latter both in the cat and rabbit.

Biffi⁵ refused to accept Pflüger's results, although supported by Hein⁶, and by Spiegelberg⁷ in his researches on the innervation of the uterus. Biffi found that neither stimulation of the peripheral end of the splanchnics nor of the dorsal cord caused any inhibition of the intestinal movements. His opinion was for some time supported by Brown-Séguard⁸, who, however, finally declared himself convinced of the accuracy of Pflüger's results.

Mayer and von Basch⁹ in 1870, and later v. Basch¹⁰ alone, accepted the inhibitory action of the splanchnic, but stated that this was dependent on the vaso-constrictor fibres contained in the splanchnic,

¹ *Die Physiologie des Menschen.*

³ *Zeitschr. f. rat. Med.* 1857.

⁵ *Ann. univ. di med.* 1857.

⁷ *Arch. f. rat. Med.* II. 1857.

⁹ *Wiener Med. Jahrb.* 1871.

² *Sitzungsab. d. Wiener Akad.* 1857, xxv.

⁴ *Beiträge z. Phys. d. Darmbewegung.*

⁶ *Arch. f. phys. Heilk.* 1857.

⁸ *Journ. de la Phys.* 1858, p. 421.

¹⁰ *Wiener Med. Jahrb.* 1873.

since excitation of this nerve caused constriction of the intestinal vessels at the same time as inhibition of the movements. This view was opposed by van Braam Houckgeest¹ (1874) on the ground that injury to the vaso-motor fibres of the intestine did not affect the inhibitory action of the splanchnic.

Ehrmann² (1885) enunciated a new theory, viz., that the circular and longitudinal coats of the intestine were innervated in such a manner that stimulation of the splanchnic caused contraction of the longitudinal coat, but at the same time lengthening of the circular fibres. He concluded therefore that the splanchnic was a motor nerve for the longitudinal, but inhibitory for the circular coat.

Bechterew and Mislawski³ (1889) obtained both motor and inhibitory effects on the intestine by excitation of the splanchnic, though inhibition was the more marked. They also showed that fibres for the small intestine pass out in the 6th to the 13th dorsal roots and in the 1st lumbar, while for the large intestine they pass out in the remaining lumbar and first three sacral roots.

Jacobj⁴ (1891) was led to believe that the suprarenals send inhibitory fibres to the intestine, and that if intestinal movements are first produced by vagus stimulation, excitation of the suprarenals stops them. This result was said not to be due to spreading of the current to the splanchnics.

Steinach⁵ (1893) carried out a series of experiments on frogs to determine the nerve outflow to the intestine from the spinal cord. Stimulation of the peripheral ends of certain posterior roots caused contraction of the small intestine. These posterior roots were the 4th, 5th and 6th. The anterior roots he found to have no effect on the small intestine. The posterior roots also produce effects on the vaso-motor nerves of the intestine, as Stricker, and also Morat, found in warm-blooded animals.

Pohl⁶ (1894) performed some experiments on rabbits, and found that the rhythm of the intestinal movements was not influenced by

¹ *Pflüger's Archiv*, vi.

² "Ueber die Innervation des Dünndarms." *Wiener Med. Jahresbericht*, 1885.

³ "Ueber centrale u. periphere Darminnervation." *Arch. f. Phys.* 1889.

⁴ *Arch. f. exp. Pathol.* xxix.

⁵ "Ueber die motorische Innervation des Darmtractus durch die hinteren Spinalwurzeln." *Lotos*, 1893, Sep.-Abdr.

⁶ "Ueber Darmbewegungen u. ihre Beeinflussung durch Gifte." *Arch. f. exp. Pathol.* xxxiv.

stimulation of the splanchnic, but that stimulation of the mesenteric nerves caused inhibition of the rhythm.

Courtade and Guyon¹ (1897) found that, in a curarised dog stimulation of the undivided splanchnic in the thorax produced contraction of the circular and inhibition of the longitudinal coat of the intestine. Excitation of the peripheral end of the divided splanchnic gives the same result, as also does excitation of the central end of the divided nerve—reflexly. This cannot be explained by assuming it to be a vaso-motor effect, for though this might account for the inhibition of the longitudinal, it could not explain the contraction of the circular coat; and, moreover, excitation of both the central and peripheral ends of the splanchnic gives the same result, whereas, in the case of vaso-motor nerves, stimulation of the central end causes vaso-dilatation, stimulation of the peripheral end vaso-constriction of the intestinal area. These results of Courtade and Guyon are in direct opposition to those of Ehrmann, who holds that the splanchnic is a motor nerve for the longitudinal instead of for the circular fibres, and inhibitory for the circular instead of for the longitudinal fibres, as the latter observers maintain. Courtade and Guyon find, however, that when traction has been made on the mesentery, or after the animal's death, they obtain the result which has been considered by Ehrmann to be normally present—contraction of the longitudinal and inhibition of the circular coat—on stimulating the splanchnic. When this result is obtained it may be *followed* by the contrary effect, thus showing that the splanchnic contains both motor and inhibitory fibres.

Vagus. Remak² (1858) found that stimulation of the vagus caused movements of the stomach and large intestine. A similar result was also obtained by E. Weber³. Pflüger⁴ (1855), however, saw sometimes an increase, sometimes a diminution of the intestinal movements on vagus stimulation. Pincus (1856)⁵ and also Panum⁶ found that intestinal movements continued after section of both vagi. Budge⁷ (1869) showed that in the rabbit contraction of the stomach, intestine and cæcum was produced by stimulation of the vagi. If the vagi were cut, excitation of the medulla oblongata no longer caused contraction of the intestine, as was the case when they were intact. Nasse⁸ (1866) also

¹ *Arch. de Phys.* April, 1897.

² *Müller's Archiv*, 1858.

³ *Wagner's Handwörterbuch der Physiologie.*

⁴ *loc. cit.*

⁵ "Exper. de vi nervi vagi et symp." Diss. Vratisl. 1856.

⁶ *Schmidt's Jahrbuch*, 1856.

⁷ *Lehrbuch der spec. Phys.* 1869.

⁸ *loc. cit.*

found that stimulation of the vagus affects the whole intestinal canal, though in dogs of five weeks old it has no effect.

Mayer and v. Basch¹ (1871) found that vagus excitation caused sometimes increased contraction, sometimes not—increase occurring if the blood in the intestine was venous, and a short time before or after death. They quote some results obtained by Legros and Onimus, showing that in dogs excitation of the vagus has no effect on the intestine, though contraction results if artificial respiration be stopped during stimulation and asphyxia allowed to supervene.

Sanders² (1871) found that the intestinal contractions, which are set up in an asphyxiated animal, cease on section of the vagi. But stimulation of the peripheral end of the vagus still causes contraction. Van Braam Houckgeest³ (1874) showed that excitation of the vagus causes intestinal contraction, especially after section of the splanchnics, while Ludwig and Kupffer found that simultaneous excitation of the splanchnic prevented the vagus effect being seen.

Paschkis⁴ (1883) obtained contraction of the intestine on vagus stimulation, as determined by direct observation. It having been suggested that the intestinal contractions were due to inhibitory action of the vagus on the heart, a kymograph was employed at the same time, and it was found that stimuli strong enough to cause only a slowing of the cardiac contraction, and not a definite stoppage, still produced contraction of the intestine. Compression of the thoracic aorta also caused no intestinal contraction. Stimulation of the vagus in the thorax was not employed.

Ehrmann⁵ (1885) found that stimulation of the undivided vagus caused lengthening of a segment of intestine, with a long latent period and a long after-effect, but also at the same time shortening of the circular fibres with a short latent period.

Pal and Berggrün⁶ (1888) found that excitation of the peripheral end of the vagus frequently caused intestinal contractions, but that if the cervical cord be first divided, this always occurs, and they argued that there was a spinal inhibitory centre for vagus action.

Bechterew and Mislawski⁷ (1889) thought that the vagus contained both motor and inhibitory fibres for the intestine, but that the former predominated.

¹ *Wiener med. Jahrb.*

² *Centralblatt f. d. med. Wissensch.* 1871.

⁴ *Med. Jahrb. d. Ges. d. Aerzte in Wien*, 1883.

⁶ *Ibid.* 1888.

³ *Pflüger's Archiv*, vi.

⁵ *Ibid.* 1885.

⁷ *Arch. f. Phys.* 1889.

Jacobj¹ (1891) considered the vagus to be a motor nerve for the intestine, but he thought that one vagus acted more powerfully on the stomach, the other on the intestine. Which vagus it was that produced the greatest effect on the intestine varied in different cases.

Morat² (1893) made use of his method of 'ampoules conjuguées' to prove that the vagus was an 'augmentor' nerve for the stomach.

Pohl³ (1894) states that vagus excitation does not affect the rhythm of intestinal movements. The protocol of one experiment only is given, but in it stimulation of the vagus at the cardia with the coil at 13 cm. causes stronger contractions and a quickening of the rhythm, at one time from 13 to 15, at another from 13 to 18 per minute.

Courtade and Guyon⁴ (1897) state that stimulation of neither vagus has ever in their hands given contraction of the circular coat of the intestine.

Method.

The method adopted in this investigation was one suggested by Professor Schäfer, which enables the movements of the intestine to be recorded without exposing it to changes of temperature, and allows the intestine to remain in the abdominal cavity, under conditions as little as possible abnormal. All interference with nervous and vascular supply is avoided. The intestinal movements are recorded on a smoked revolving drum by a sensitive piston-recorder, or a tambour, connected with a tube which is inserted into a short length of gut, isolated from the rest of the intestine by ligatures. These are so applied that the nervous and vascular supply are not interfered with. A little warm oil or salt solution just sufficient to keep the gut uncollapsed is put into the tube. The various experiments have included portions of the small intestine from the pylorus to the ileo-cæcal valve.

Normal movements and effect of drugs.

The normal movements of the small intestine have been not inaptly described as 'Pendel-bewegungen,' since the total effect of the contraction of the muscular coats, acting upon the intestine as it hangs free in the abdominal cavity, imparts to it a to and fro movement. This

¹ *Arch. f. exp. Pathol.* xxix. pp. 171—211.

² *Arch. de Phys.* 1893, pp. 142—153.

³ *Arch. f. exp. Pathol.* 1894.

⁴ *Arch. de Phys.* 1897.

movement is chiefly due to the projection forward of the coil of intestine by the contents entering it from above, and its subsequent retraction after it has itself contracted on these contents and again become empty. These normal movements vary both in extent and in duration, not only in different animals, but also in the same animal under different conditions. The variations in extent are much greater than the variations in rhythm, which is often fairly constant, and when the intestine is contracting normally, alternate contraction and dilatation recurs at intervals of five seconds. The waves vary from being almost imperceptible to large and prolonged curves. Morphia has no appreciable effect upon the movements when given in small doses, though v. Vamossy¹ has shown that in doses of 40 mg. intravenously it has an inhibitory action, and when injected directly into the intestine it has a direct peripheral effect. This differs from Nothnagel's² view that morphia in small doses increases the tonic splanchnic inhibition of the intestine, but in larger doses prevents this inhibition—a view which is supported also by Pal and Berggrün³ from experiments of their own. Binz, Filehne and others think that morphia first affects the nerve terminations, and later the ganglia in connection with the intestine; while Spitzer⁴

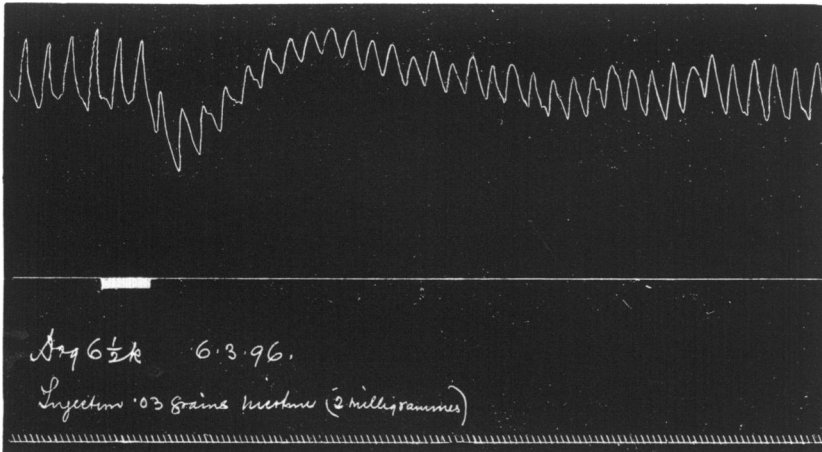


Fig. 1. Dog, 6½ k. Effect on intestine of injection of 2 milligrammes of nicotine intravenously.

¹ *Deutsch. med. Wochenschr.* 29.

² *Virchow's Archiv*, 88.

³ *Arbeiten a. d. Inst. f. allg. u. exp. Pathol. in Wien*, 1890.

⁴ *Virchow's Archiv*, 123.

modified Nothnagel's theory, and ascribed the action of morphia to stimulation of an inhibitory centre, and at the same time diminution of sensibility to local stimulation. Pohl¹ found that in the rabbit doses even of 80 milligrammes of morphia did not affect the normal reflex excitability of the intestine, nor did they paralyse the splanchnic. In dogs and cats we have not experimented with doses larger than from 15 to 20 milligrammes. Small doses of curari injected intra-

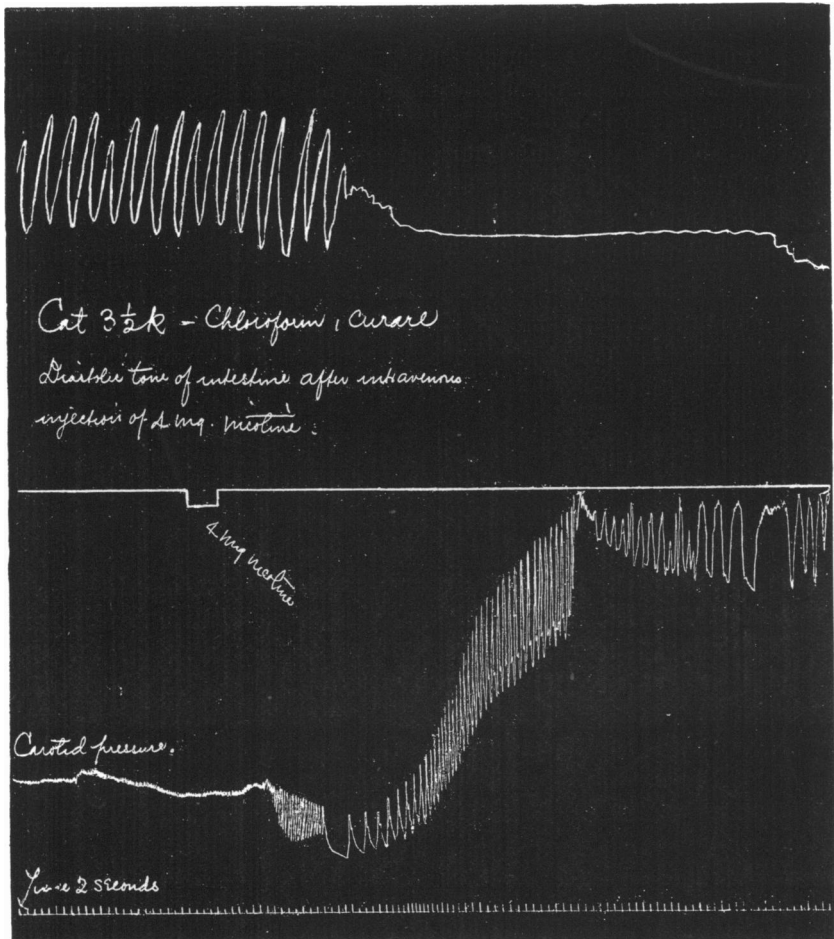


Fig. 2. Cat, 3 1/2 k. Diastolic tone of intestine after intravenous injection of 4 mg. nicotine.

¹ Arch. f. exp. Pathol. 34.

venously have not been found to produce any effect upon the rhythm of the intestine. Nicotine has the most marked action of any drug with which we have experimented; even in very minute doses it profoundly affects the intestinal tone, causing in some animals systolic tone, though the rhythmic intestinal movements may continue at the same rate as before (Fig. 1). In other animals equally marked diastolic tone is produced (Fig. 2), the result obtained always coinciding with that seen on stimulation of the splanchnic. Fig. 3 shows the diastolic

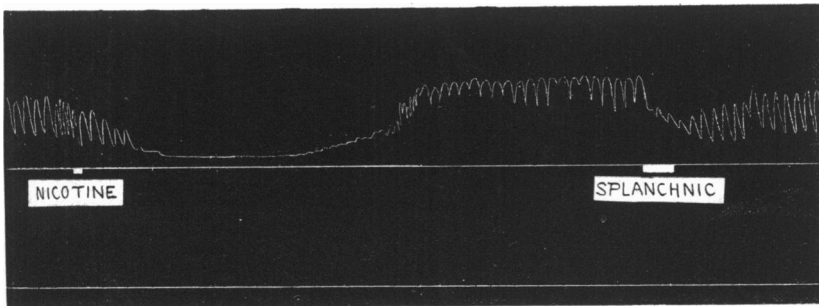


Fig. 3. Dog, in which intravenous injection of 1 mg. nicotine and stimulation of the left splanchnic respectively produced diastolic tone of the intestine, the rhythmic beats being diminished on splanchnic excitation, but abolished by the nicotine.

tone produced in a dog both by stimulation of the splanchnic and by injection of nicotine. The former causes a diminution of the rhythmic beats, while the dose of nicotine abolishes them entirely.

The effect of nicotine is of interest as showing that the intestinal tone is not dependent on the blood-pressure, for in all cases nicotine causes a rise of blood-pressure, but it may cause either systolic tone or diastolic tone of the intestine. This is also seen in the case of splanchnic stimulation, for excitation of the splanchnic may cause at one time systolic tone, at another time diastolic tone of the intestine, but always rise of blood-pressure. In Fig. 17, excitation of the spinal cord causes first systolic tone of the intestine accompanied by rise of pressure, but this is succeeded by very marked diastolic tone without a corresponding fall of blood-pressure. These results are in accordance with the views previously mentioned of van Braam-Houckgeest and of Courtade and Guyon.

Suprarenal extract freshly prepared has been injected intravenously

in a few animals, and has always been found to produce systolic tone in dogs. Fig. 4 shows the effect on the intestine and on the kidney volume

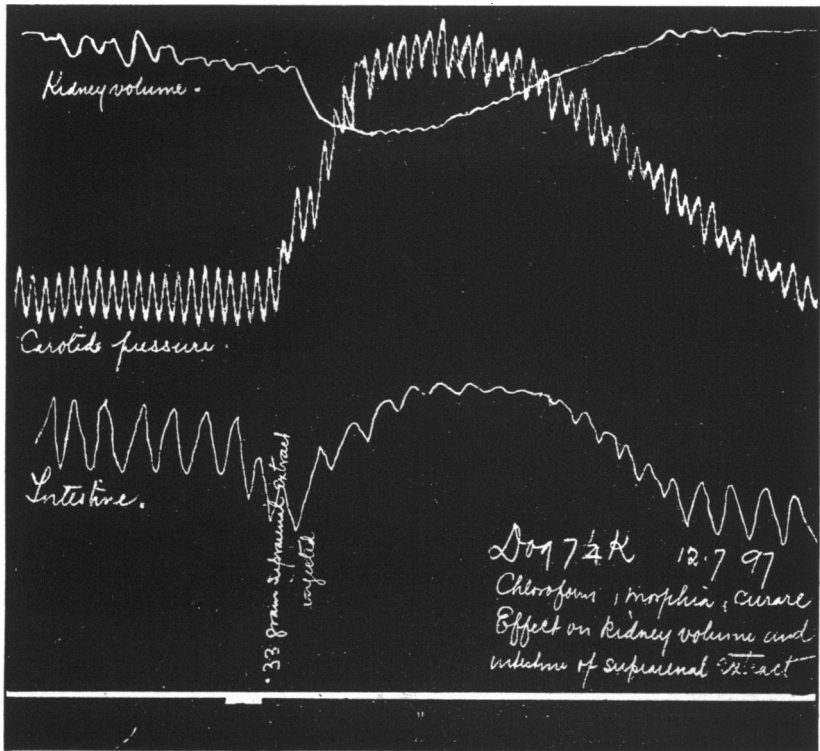


Fig. 4. Dog. Effect on kidney volume (upper tracing), blood pressure, and intestine (lower tracing), of intravenous injection of suprarenal extract.

of injecting 22 mg. of suprarenal extract intravenously, as determined by placing the kidney in a plethysmograph, such as that employed by Schäfer and Moore for the spleen¹.

Influence of various nerves.

When the small intestine is removed from the body, and its connection with the central nervous system therefore abolished, movements of an apparently spontaneous nature may be observed, or if not apparent may be excited by direct stimulation. The

¹ This *Journal*, xx. p. 1. 1896.

movements may be modified within the body by stimulation both of the central nervous system and of peripheral nerves. Inasmuch as the vagus is usually described as the principal *motor*—or, preferably, *augmentor*—nerve, particular attention has been paid to its action. It has, as a rule, been stated, that stimulation of the peripheral end of the cut vagus causes contraction of the intestine and increase of the rhythmic movements, but quite recently Courtade and Guyon¹ have denied that the vagus has any action on the circular coat of the intestine. In our experiments neither stimulation of the central nor of the peripheral end of the cut vagus has had any effect upon the intestinal movements. The vagi have been stimulated on both sides, in the neck and in the thorax, with currents of different strengths and with different rates of repetition of the stimulus. When the cervical vagus was stimulated, minute doses of atropine were as a rule given, so as to eliminate as far as possible the action of the vagus on the heart, and even when the thoracic vagus was stimulated, atropine was also in some cases given. All our experiments show that such doses have no effect upon either the intestinal rhythm or upon the nerves which pass to the intestine. In each case the nerve was divided, and both central and peripheral ends stimulated, but in 24 out of 25 animals experi-

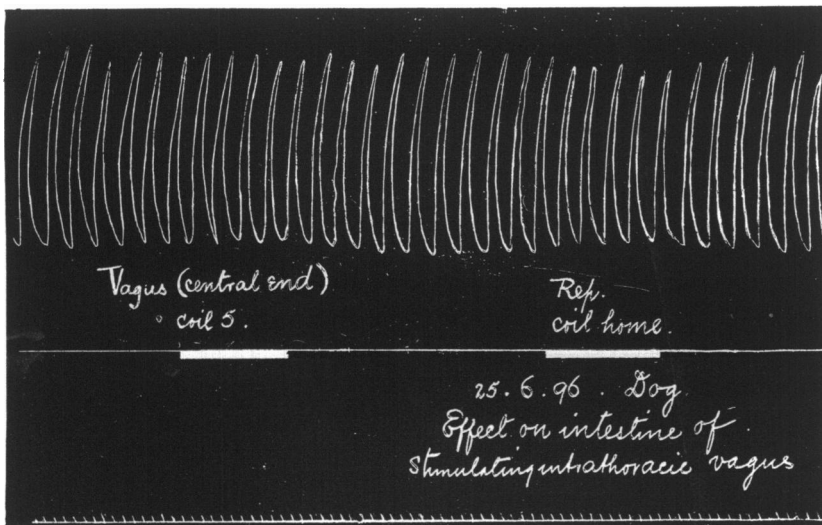


Fig. 5. Dog. Stimulation of central end of cut intrathoracic vagus with strong current.

¹ *loc. cit.*

mented on, which included dogs, cats and rabbits, the stimulation did not cause any contraction of the intestine or any increase of the normal rhythmic movements. Fig. 5 illustrates this. Having regard to the possibility of the intestine being influenced by the anæsthetic used, this was varied in several different ways, but without altering the result. The action of the vagi was in every case confined entirely to the stomach.

In one case only (dog) there occurred a diminution in the extent of the movements accompanied by a strong diastolic tone (Fig. 6). It is

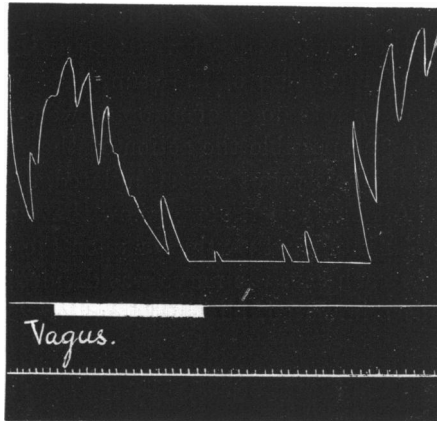


Fig. 6. Dog, in which stimulation of the peripheral end of the thoracic vagus gave an exceptional effect. This consists of inhibition and diastolic tone beyond the power of the tambour to record. Vagus shown to terminate chiefly in solar plexus.

possible that this effect was produced by a pull exerted upon the small intestine by the contraction of the stomach, but this did not seem to us to be the case. It was found on post-mortem dissection that in this case the vagi were distributed mainly to the celiac plexus, and that but a small proportion of the nerves passed to the stomach.

The splanchnic has usually been regarded as an inhibitory nerve for the intestine, and it is true that it contains inhibitory fibres, more especially in the *cat*. In this animal, excitation of either splanchnic has *always* caused diastolic tone of the intestine, with a tendency to diminution in the extent of the normal rhythmic contractions, which may quite disappear during the excitation (Fig. 7).

In the *dog*, however, excitation of the splanchnic almost always causes systolic tone of the intestine. The normal rhythmic con-

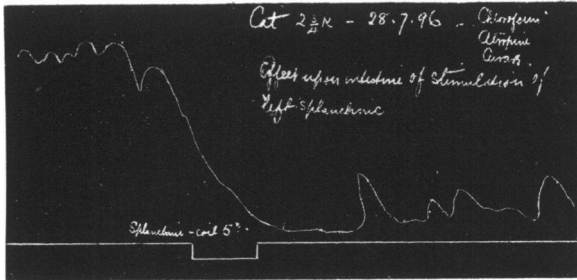


Fig. 7. Effect upon intestine of stimulation of left splanchnic, coil at 5.

tractions are usually continued during the excitation, and are seen as small superposed waves upon the tracing (Fig. 8). In some cases,

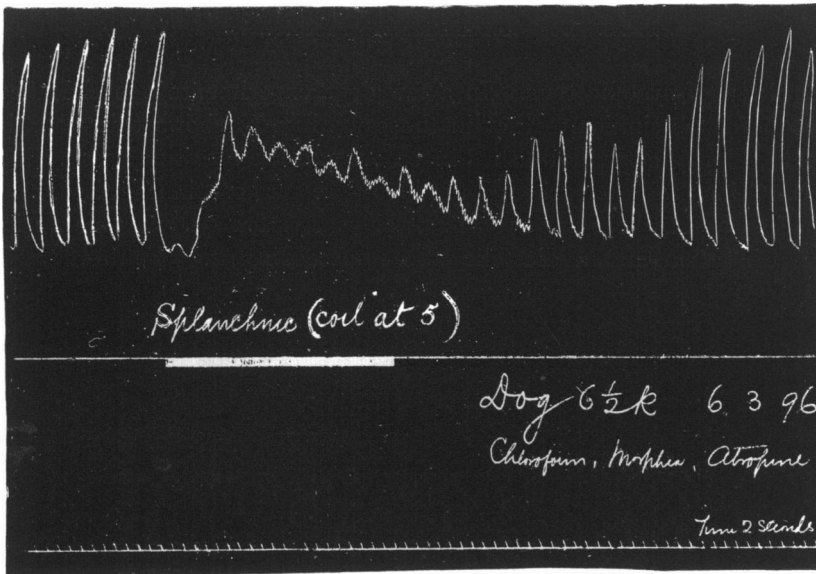


Fig. 8. Dog. Excitation of splanchnic, coil at 5.

however, no such superposed waves are seen, and the tracing shows merely a single tonic contraction of greater or less range (Fig. 9).

The effect is usually followed by diastolic tone, and occasionally diastolic tone may for a short time actually precede as a first effect a more lasting

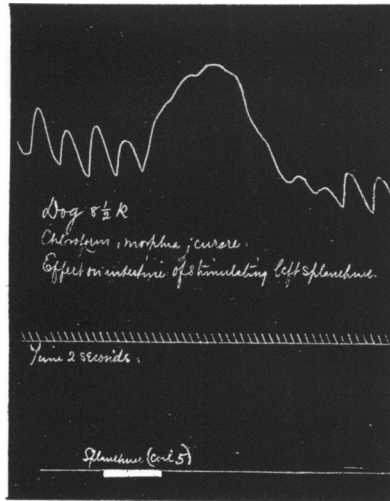


Fig. 9. Dog. Stimulation of splanchnic, coil at 5.

condition of systolic tone. In a few dogs experimented on the effect produced was similar to that in the cat. Fig. 10 shows this well, the beats being greatly diminished in extent and the intestine passing into a condition of diastole, though the blood-pressure continues raised.

In Fig. 11 there are two effects shown, viz., a systolic tone during the excitation and a diastolic effect succeeding it. We have made

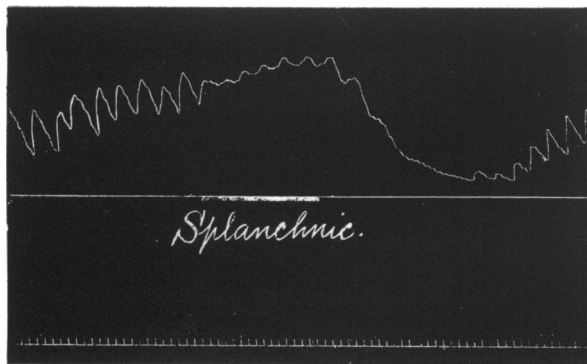


Fig. 11. Dog. Stimulation of splanchnic, coil at 5.

several attempts, by stimulating the splanchnic in the thorax at extremely slow rates and with very different strengths of current, to

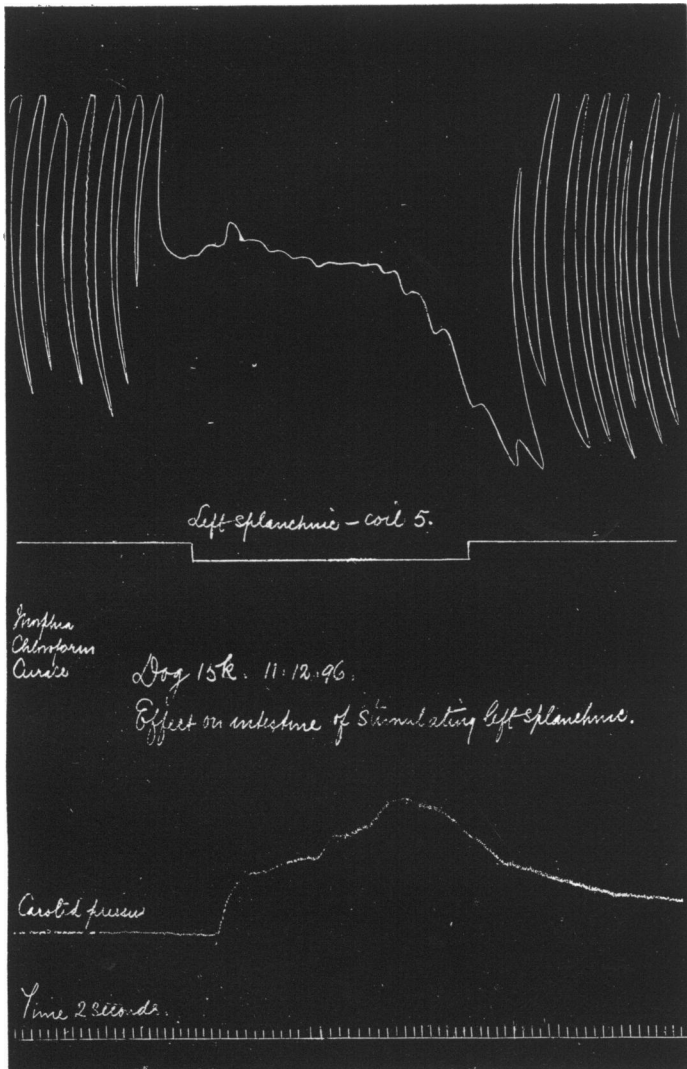


Fig. 10. Dog. Stimulation of splanchnic causes diastolic tone.

determine whether we could in the dog produce at will a systolic or diastolic effect. Such attempts have not been successful, as is shown

in Fig. 12, when excitation even at the rate of 1 per second still caused systolic tone. We are therefore led to believe that the final result of

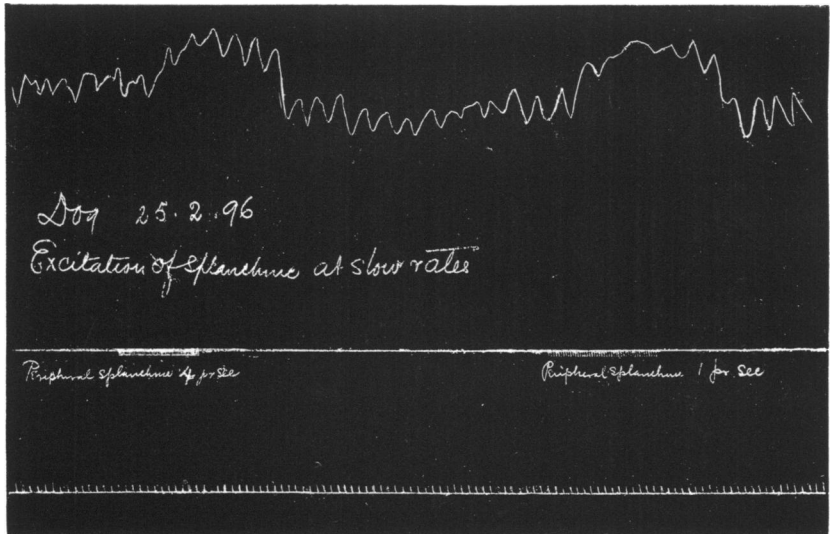


Fig. 12. Dog. Stimulation of splanchnic at rates of 4 per second and 1 per second respectively.

excitation depends upon the relative proportion of the different fibres contained in the nerve, rather than upon the method of excitation of the nerve. No difference has been observed between the results obtained from stimulation of the right and left splanchnic respectively. In the rabbit, the effect of splanchnic stimulation was found to be the same as in the cat.

In stimulating the peripheral end of the cut greater splanchnic, it must be remembered that it receives a branch from the lesser splanchnic, and that unless this is divided the result may be complicated by reflex effects. It is possible that this has been overlooked in many of the results previously published.

In one experiment (dog) where the semilunar ganglion was exposed and directly stimulated, the same effect was obtained as on stimulation of the splanchnic within the thorax.

Excitation of the nerves accompanying the mesenteric arteries gives an effect similar to that obtained on stimulation of the splanchnic in the same animal.

On the nerve outflow to the intestine from the spinal cord.

The effects on the intestine of stimulating the anterior nerve-roots have been investigated both in dogs and cats. The animals were anaesthetised, and a minimal dose of curare given, artificial respiration being employed during the whole of the experiment. The animal was placed upon a tin of hot water, and warm air was pumped into its lungs. An incision was made some six inches long over the spines which were to be removed, and the incision carried through the skin and subcutaneous tissue down to the spines. The vertebral aponeurosis was then cut through on each side of the spines, the erector spinæ exposed and separated from the bone, attention being paid to the prevention of hæmorrhage as far as possible. The dorsal branches of the intercostal arteries were tied, and the hæmorrhage from smaller vessels stopped with sponges and hot lotion. The spines and neural arches were then rapidly removed with bone forceps, care being taken not to injure the cord in any way. The nerve-roots being exposed as they passed outwards to the intervertebral foramina were tied with threads of different colours, and divided centrally to the ligature. These nerve-roots were stimulated from above down with a faradic current. The results obtained were similar to those obtained on excitation of the splanchnic, *i.e.* in the *dog*, systolic tone, and in the *cat*, diastolic tone with diminution of the normal rhythmic contractions. In no case have we obtained effects on stimulating nerve-roots higher than the 6th thoracic. In one case only (*dog*) there appeared to be a slight effect on stimulating as low as the 5th lumbar¹ (fig. 15), but the sharpest and most extensive effect was obtained on stimulation of the 8th thoracic to the 1st lumbar, and the effect was about equally marked with the roots of the two sides. Figs. 13 and 14 are from a *dog*, and show the marked systolic tone which was obtained on stimulation of the 14th post-cervical and 10th post-cervical roots respectively, the first on the right side, the second on the left. Fig. 16 is from a *dog*, and shows an exceptional effect on stimulation of the 9th post-cervical nerve-root. The first effect is the normal systolic tone, but this is succeeded by strongly marked diastolic tone, the full extent of which the piston-recorder was incapable of registering.

¹ The 5th lumbar-root was found by Langley (*This Journal*, xii. *Proc. Physiol. Soc.*) and by Langley and Anderson (*This Journal*, xviii.) to be the lower limit of the thoracic-lumbar outflow of fibres to the large intestine of the rabbit.

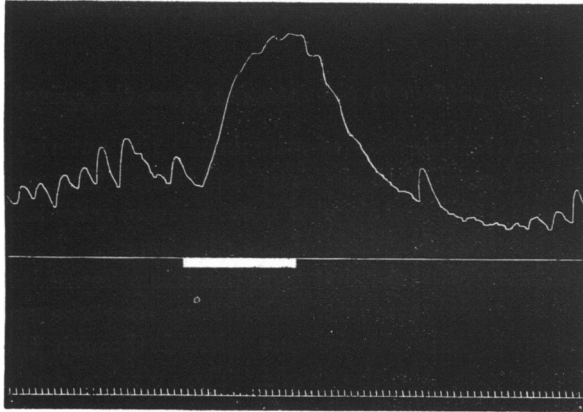


Fig. 13. Dog. Stimulation of 14th right post-cervical nerve-root, coil at 5.

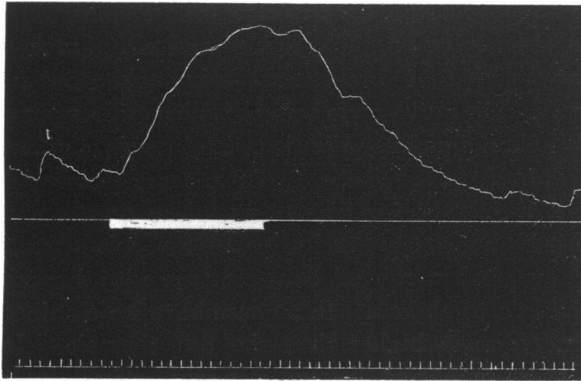


Fig. 14. Dog. Excitation of 10th left post-cervical nerve-root, coil at 5.

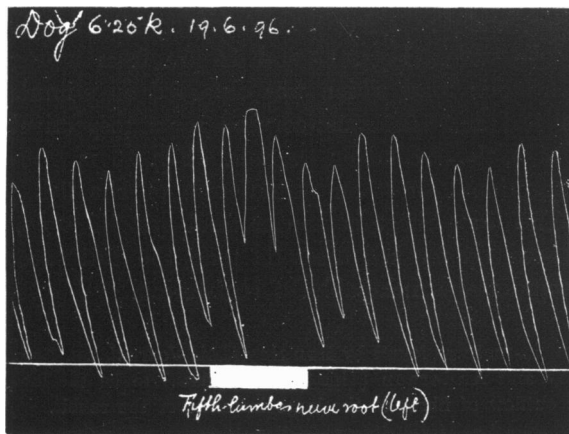


Fig. 15. Dog. Stimulation of 18th left post-cervical nerve-root.

Stimulation of the cut spinal cord between these roots was contrasted with the effects obtained on stimulation of the splanchnic, by arranging the apparatus so that the same current could be switched on to one or other alternately. Needle electrodes were inserted, one into the upper, and one into the lower extremity of the divided segment

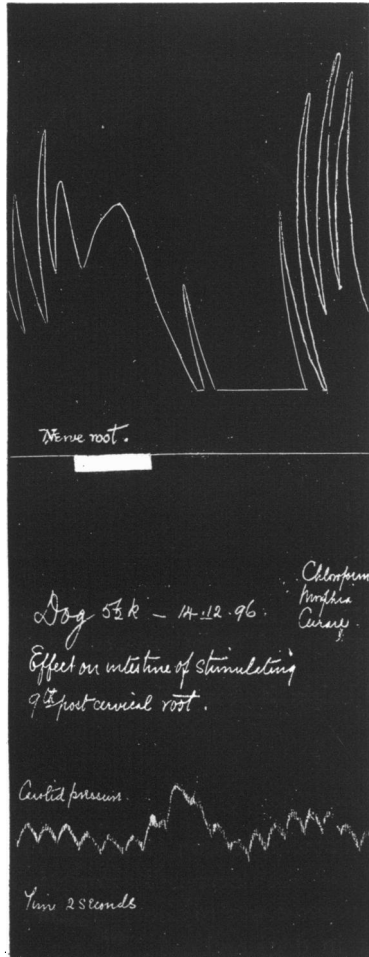


Fig. 16. Dog. Stimulation of 9th post-cervical root. The full extent of the diastolic tone could not be recorded by the tambour.

of spinal cord, and a current could thus be sent through the entire segment. It was then found that, both in the dog and cat, the same

effect was obtained on stimulation of the spinal cord as on excitation of the splanchnic. Fig. 22, taken from a dog, is an illustration of

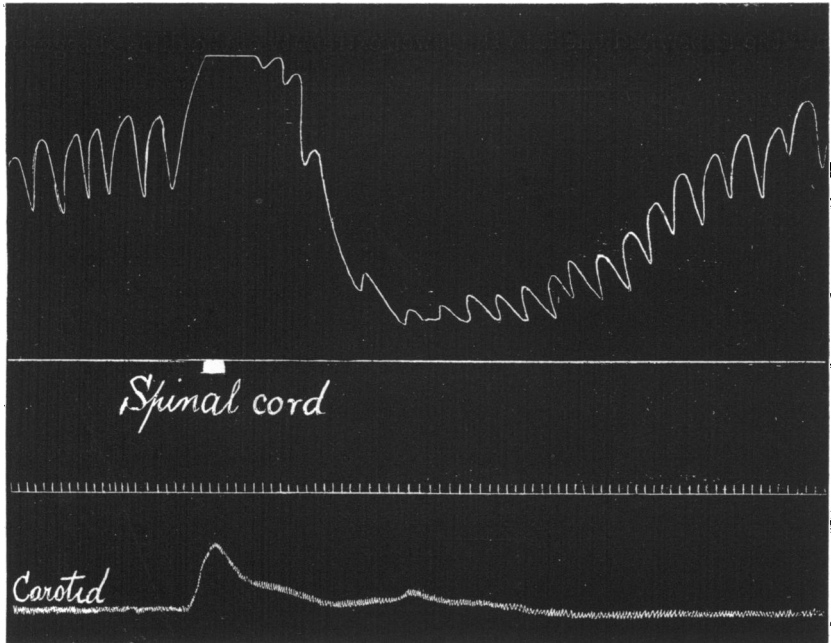


Fig. 17. Dog. Effect of stimulating the segment of spinal cord between the 7th and 12th post-cervical vertebræ. The marked after-effect seen in the case of the intestine is not accompanied by any corresponding alteration in blood-pressure.

this, the after-effect being however less marked in the case of the splanchnic.

On the nerve-cell connections of the intestinal visceromotor fibres.

By means of intravenous injection of nicotine it has been sought to determine the situation of the nerve-cell connections of the fibres which pass from the spinal nerve-roots to the intestine. These experiments have been carried out in dogs and cats. The animal was anæsthetised and curarised, and the movements of the intestine recorded by the method previously described. In the earlier experiments a laminectomy was performed, the cord exposed, and some nerve-roots (right side) which were known on excitation to produce an effect upon the intestine ligatured and divided close to the cord. The segment of spinal cord

exposed was then removed. The left splanchnic was exposed in the thorax, ligatured and divided. The nerves accompanying the mesenteric artery to the segment of intestine under observation were isolated and placed upon paraffin-guarded electrodes and returned to the abdomen. In some cases a blood-pressure tracing was taken at the same time. The effects upon the blood-pressure and the intestine of stimulating severally the nerve-root, splanchnic and mesenteric nerves were recorded. Small doses of nicotine were then injected intravenously, beginning with one milligramme, the above effects being again recorded after each injection. Successive doses of nicotine were subsequently injected. In the later experiments this method was modified in the following way. A small area of cord was exposed in the lower dorsal region and cut through above and below. One guarded needle-electrode was placed in the upper end of the severed portion, and another in the lower end, so that a strong faradic current could be sent through the entire segment of the cord. The left splanchnic was exposed as before, and nicotine injected in successive small doses. The contraction resulting from stimulation of the nerve-root or of the spinal cord gradually diminished after each successive injection of nicotine, as did also that obtained on stimulation of the splanchnic, until finally such excitation no longer produced any effect upon the intestine. Stimulation of the mesenteric nerves still caused marked systolic tone of the intestine. The diminution produced by successive small doses of nicotine affected equally the results obtained by stimulation of the splanchnic and spinal cord, until these effects disappeared simultaneously. The effect on the blood-pressure produced by this excitation in some cases survived after all effect on the intestine had disappeared, and there is reason to think that the intestinal visceromotor fibres are more susceptible to the action of nicotine than are the vaso-motor fibres. The amount of nicotine required to abolish the effect on the intestine was in all cases small, and seldom exceeded 8 milligrammes in dogs of 5 to 10 kilos. The nicotine was freshly prepared and was supplied by Martindale. The conclusion therefore is that there is no cell-station in the course of the nerves between the spinal cord and the nerve-cells of the solar plexus. This is in accordance with the general principle laid down by Langley¹, that there is only one cell station interpolated in the course of the fibres passing to the viscera from the spinal cord, and that this is peripheral to the ganglia of the chain of the sympathetic, and contrary

¹ *A short account of the sympathetic system*, 1895. See also this *Journal*, xx. 1896.

to the results obtained by Schäfer and Moore in the case of the spleen nerves¹. We are not yet in a position to elucidate the cause of this difference. Our effects were obtained with far smaller doses of nicotine than those employed by Langley.

CONCLUSIONS.

1. The small intestine of the dog, cat, and rabbit shows normally a regular rhythm of contraction and dilatation—systole and diastole—of variable rate and extent in different animals, but averaging in the dog about 12 per minute.

2. Besides, or independently of, these regular rhythmic contractions, the small intestine may exhibit a condition of either generally increased contraction (systolic tone), or generally diminished contraction (diastolic tone).

3. Small doses of morphia (up to 2 milligrammes per kilo body-weight) produce no appreciable effect upon the rhythm of the small intestine. The same is true for atropine.

4. Nicotine, even in very minute doses, causes in some animals (*e.g.* most dogs) systolic tone; in other animals (some dogs and all cats) diastolic tone, without necessarily abolishing the rhythmic movements. By larger doses these are temporarily abolished.

5. Stimulation of the peripheral end of the cut cervical vagus—after administration of atropine in doses sufficient to prevent cardiac inhibition—, or of the thoracic vagus, usually produces no effect upon the small intestine. In one experiment only out of 25 was there an effect produced, and this was strong diastolic tone with diminution of the rate of rhythm.

6. Stimulation of the peripheral end of the cut splanchnic of either side usually produces in dogs systolic tone, rarely diastolic tone; in cats the effect of stimulation is usually to cause diastolic tone. There is a tendency to a limitation of the excursion of the normal rhythmic movements during the excitation of the splanchnic, amounting sometimes to disappearance, but not necessarily accompanied by slowing of the rhythm, indeed, with the systolic tone there seems a tendency to increased rate of rhythm. An after-effect of increased extent of excursion together with either diastolic or systolic tone is usually observed.

¹ This *Journal*, xx. 1896.

7. The splanchnics probably contain in all animals two sets of nerve-fibres, the one set tending to produce increased contraction of the intestine (*i.e.* diminution of its calibre), the other set diminished contraction. Effects may also be produced upon the rhythmic movements (diminution in extent and quickening or slowing), but whether by the same or by different fibres from those affecting the tone cannot be stated.

8. The nerve-fibres pass to the splanchnic from the anterior roots of from the 6th thoracic to the 2nd, 3rd, 4th or 5th lumbar nerves, but the lower limit of the outflow has not been precisely determined. Stimulation of these roots produces the same effects as stimulation of the splanchnics.

9. The nerve-fibres which pass to the small intestine by the splanchnics have one cell-station in the ganglia of the solar plexus.