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THE ORIGIN OF CERTAIN NON-MEDULLATED NERVE FIBRES WHICH FORM SYNAPSES IN THE INFERIOR MESENTERIC GANGLION OF THE RABBIT

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Brown & Pascoe (1952) have shown that in the mesenteric nerves leaving the inferior mesenteric ganglion of the rabbit there is a distinct group of nerve fibres conducting at 0.25 m/sec at 20° C. These fibres were found to form synapses in the ganglion with nerves conducting at 0.45 m/sec. The post-synaptic fibres return along the same nerve trunks by which the slower fibres enter the ganglion, and, as judged by their velocity of conduction, were not different from the other postsynaptic fibres leaving the ganglion. The mesenteric nerves are composed largely of postganglionic fibres, and the slow preganglionic axons form only a small proportion of the total.

This paper describes our attempts to determine the origin of the slow fibres, chiefly by means of degenerative nerve section; we conclude that their cell bodies are situated in the peripheral nervous system, possibly in the gut. This is opposed to the accepted views of Gaskell (1916) and Langley (1921), but finds confirmation in the more recent work of Kuntz (1940) and of Job & Lundberg (1952).

METHODS

Gross anatomy and nomenclature

The inferior mesenteric ganglion of the rabbit lies in the mesocolon immediately headwards of the inferior mesenteric artery (Fig. 1). There is usually a smaller ganglion, the accessory mesenteric ganglion, attached to the main ganglion by nerve strands passing on either side of the inferior mesenteric artery. The preganglionic supply from the spinal cord consists of several fine nerves collectively called the inferior splanchnics. The most conspicuous nerves leaving the inferior mesenteric ganglion are those referred to by Langley & Anderson (1896) as the ascending mesenteric branches. These pass headwards in close contact with the inferior mesenteric vein and can be traced by gross dissection as far as the superior mesenteric artery where they divide to form a plexus mingling with the superior mesenteric nerves from the superior mesenteric ganglion.

Since we have as yet been unable to assign any particular function to the slow preganglionic fibres they are referred to in the text as the 'slow C fibres'.

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Degenerative nerve section

The rabbits were given sufficient pentobarbitone sodium solution by ear vein to render them unconscious, and then full surgical anaesthesia was obtained with open ether. Atropine sulphate, 1 mg/kg by intraperitoneal injection, was given in some cases including those where the vagi were sectioned.

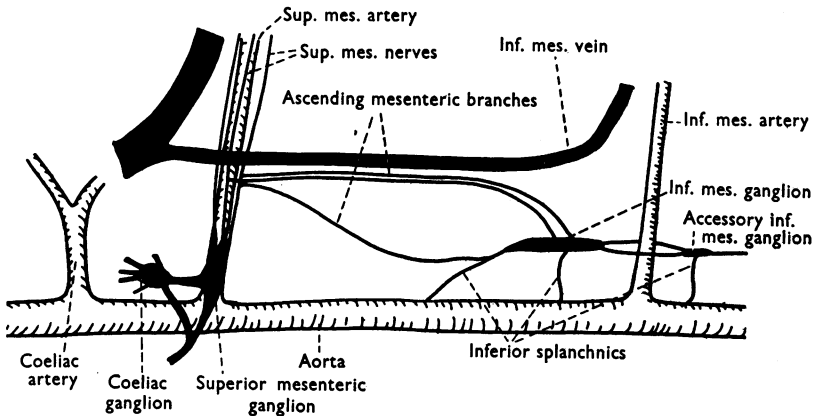


Fig. 1. Diagram to show relative positions of the inferior mesenteric, superior mesenteric and coeliac ganglia. Note ascending mesenteric branches forming a plexus on the superior mesenteric artery with strands of the superior mesenteric nerves. Animal supine, guts retracted towards left side.

Decentralization of the inferior mesenteric ganglion. The ganglion was exposed by a midline incision and the mesocolon in which it lay was lightly stretched over a black glass plate. The mesocolon between the ganglion and the abdominal aorta was cut through with a sharp knife and the inferior mesenteric artery carefully 'cleaned', so cutting all the inferior splanchnic nerves. In one rabbit the accessory mesenteric ganglion was also removed, leaving the main ganglion attached only to the ascending mesenteric branches.

Section of the ascending mesenteric branches. These nerves are closely attached to the inferior mesenteric vein and initially we attempted to divide them without damaging it. This proved difficult, and it was not possible to be certain that all of the rather diffuse strands had been cut. In later experiments the vein and nerves were cut between ligatures with no untoward effects, all the animals making uneventful recoveries.

Bilateral splanchnicotomy. The approach was through lateral incisions on each side, the splanchnics being found and cut at the level of the crura of the diaphragm.

Bilateral vagotomy. In the first two experiments the vagi were sectioned in the neck since at this level their identification is certain. Cutting both vagi in the mid-neck region is invariably fatal, through paralysis and anaesthesia of the larynx from the degeneration of the recurrent laryngeal nerves. Fortunately the recurrent laryngeal on the right side leaves the vagus just before it enters the thorax. The operation was performed in two stages. In the first, the vagus was dissected in the lower neck on the right side until the point where the recurrent laryngeal left it could be clearly seen. The vagus was cut below this level, care being taken not to damage the recurrent laryngeal nerve. In the second stage, after an interval of 1-2 weeks, the left vagus was cut in the middle neck. Since sympathetic nerve fibres enter the vagus in the thorax, in later experiments both vagi were cut in the abdomen. A midline incision from the xiphisternum was made, the stomach was pulled gently downward and the vagi found and cut on the dorsal and ventral surfaces of the oesophagus. When both vagi and splanchnics were cut in the abdomen, the vagi were approached through one of the lateral incisions used for splanchnicotomy.

Solar ganglionectomy. A left lateral incision was employed as for the approach to the left splanchnic. The guts were gently retracted towards the right side and the ganglia located near the coeliac and superior mesenteric arteries. It proved essential to avoid traction on these arteries since this very readily caused irreversible ischaemia of the guts and the animals succumbed in a few hours. The ganglia were removed intact and the arteries carefully cleaned at the same time in order to excise as far as possible any stray groups of ganglion cells.

Abdominal sympathectomy and bilateral splanchnicotomy. The approach was via a long incision through the linea alba from the xiphisternal cartilage to within 4 cm of the pubic symphysis. The guts were gently retracted to the left side, together with the right kidney, and the sympathetic chains removed from the crus of the diaphragm to the level of the iliac crests. To ensure complete removal we attempted to excise each chain in one length but were not often successful owing to its fragility. The splanchnics were cut at the level of the crus as described previously.

Degeneration time

At first 3 weeks were allowed for degeneration, this being the conventional time allowed for the degeneration of sympathetic nerve fibres. After splanchnicotomy, however, although the rabbits recovered from the immediate shock of the operation, there was a high mortality rate from the tenth day onwards. Later, it was shown that 5 days after cutting the ascending mesenteric branches the slow *C* fibres had ceased to conduct impulses when tested *in vitro*; it was therefore decided to allow 7 days for degeneration.

Recording

Unless otherwise stated in the text, all recording of action potentials was performed *in vitro* using the technique previously described by Brown & Pascoe (1952). The rabbits were anaesthetized with urethane 1.8 g/kg intravenously, and the inferior mesenteric ganglion together with the required nerves dissected out and mounted in an electrode assembly. In the intervals between recording, the preparation was immersed in Locke's solution equilibrated with 95% O₂ and 5% CO₂ mixture. For electrical recording the Locke's solution was drained, leaving the preparation suspended in air.

RESULTS

Decentralization of the inferior mesenteric ganglion

After the inferior mesenteric ganglion had been separated from its connexions with the sympathetic chain and time allowed for degeneration, stimulating the ascending mesenteric branches and leading from them nearer to the inferior mesenteric ganglion gave a response similar to that previously reported by Brown & Pascoe (1952). Fig. 2 shows the electrode positions and the potentials obtained. The large spike is due to stimulation of the postganglionic axons which make up the bulk of the nerve, and it is immediately followed by the small deflexion from the slow *C* fibres. The volley from these fibres on reaching the ganglion sets up a postsynaptic discharge which returns along the nerve, and the potential due to this is seen in Fig. 2, about 150 msec after the initial action potential complex. Clearly, decentralizing the inferior mesenteric ganglion does not lead to the degeneration of the slow *C* fibres, and hence they cannot be collaterals of preganglionic fibres entering the ganglion via the inferior splanchnic nerves.

Section of the ascending mesenteric branches

The ascending mesenteric branches were cut about 4–5 cm from the ganglion. After degeneration, the ganglion with the ascending mesenteric branches and usually an inferior splanchnic nerve were tested *in vitro*. Maximal stimulation of the ascending mesenteric branches gave in this case a simple action potential. There was no deflexion due to the slow *C* fibres and hence no outcoming volley

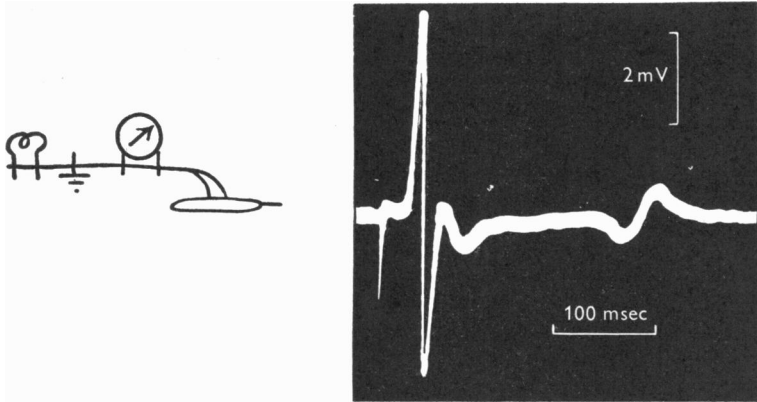


Fig. 2. Compound action potential obtained by stimulating and leading off from the ascending mesenteric branches as shown in the diagram on the left. The ganglion had been decentralized 21 days previously. Note the main spike followed by a smaller deflexion due to the slow *C* fibres. The outcoming volley of opposite phase to the main spike is seen about 150 msec later. In this and all subsequent figures a downward deflexion indicates negativity of the recording electrode nearer to the ganglion.

from the ganglion (Fig. 3). The absence of an outcoming volley cannot be taken as confirmation of the degeneration of the slow *C* fibres since the operative procedure had necessarily cut the axons of the postganglionic neurones, and as has been shown by Brown, McLennan & Pascoe (1952) this renders their cell bodies inexcitable by preganglionic stimulation. Confirmation was obtained in the following way. The ascending mesenteric branches were cut close to the inferior mesenteric ganglion. After degeneration, a length of nerve headwards of the section was stimulated *in vitro* and the action potential recorded. The potential obtained is shown in Fig. 4. The main spike as seen in Figs. 2 and 3 is almost completely absent, and in the two other experiments of the series there was no sign of it at all. The velocities of conduction of the small spike present in each of the three cases at 18° were found to be 0.28, 0.25 and 0.25 m/sec respectively. The values reported by Brown & Pascoe for the velocities of the slow *C* fibres fall between 0.21 and 0.28 m/sec. There can be no doubt from the close agreement that the small spikes remaining in the three experiments were due to the slow *C* fibres and therefore their cells of origin must lie on the headward distribution of the ascending mesenteric nerves.

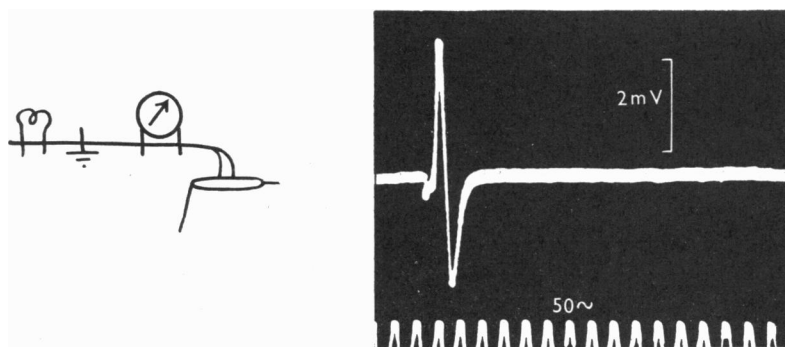


Fig. 3. Simple action potential obtained by stimulating and leading off from the ascending mesenteric branches as shown in the diagram on the left. The ascending mesenteric branches had been cut headwards of the stimulating electrodes 21 days previously. Contrast with Fig. 2. and note absence of slow *C* fibre deflexion and of outcoming volley.

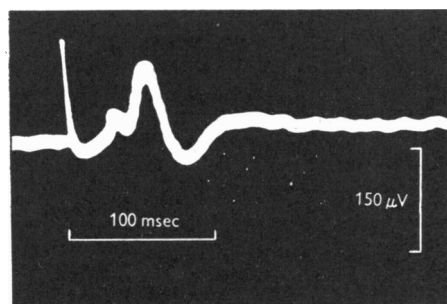


Fig. 4. Action potential obtained from a length of the ascending mesenteric branches that had been separated from the inferior mesenteric ganglion 21 days previously. The main spike seen in Fig. 2. is almost absent, the larger potential being due to the slow *C* fibres.

Degenerative section of the autonomic outflows

Splanchnicotomy. This had no effect on the size of the slow *C* fibre spike or on the outcoming volley which it set up. It seemed unlikely therefore that the slow *C* fibres enter the abdomen in the thoracic splanchnics. A further pointer to the same conclusion was obtained in those experiments where 7 days only were allowed for degeneration. Govaerts (1935, 1939) showed that division of preganglionic fibres causes a spontaneous discharge of their postganglionic connexions starting at the third day and becoming most prominent at the eighth. This spontaneous activity is seen *in vitro* and may be used for tracing the pathways of preganglionic axons. We first observed a spontaneous discharge *in vitro* from a preparation of the inferior mesenteric ganglion in which some of the ascending mesenteric branches had been cut 5 days previously.

When an uncut ascending mesenteric branch was placed on the electrodes a continuous nervous activity was apparent. This was only just visible above the noise level of the amplifier, but it could be reversibly eliminated by cooling the nerve between the ganglion and the lead off electrodes. Brown & Pascoe (1952) found no evidence that the ascending mesenteric branches contained preganglionic axons other than the slow *C* fibres, so it is reasonable to assume that sectioning these fibres leads to spontaneous activity from their post-ganglionic connexions. In five experiments where the splanchnics had been cut 7 days previously a careful search was made for spontaneous activity in the ascending mesenteric branches. It was only found in one instance which suggests that in the other four cases none of the slow *C* fibres had been interrupted by splanchnicotomy. It is likely also from the results of solar ganglionectomy that the single rabbit in which spontaneous activity was seen had suffered damage in the region of the superior mesenteric artery.

Vagotomy. Bilateral vagotomy in the neck did not abolish the deflexion due to the slow *C* fibres when the ascending mesenteric branches were stimulated, and the normal outcoming volley from the inferior mesenteric ganglion was still observed. In the two animals of this series 3 weeks were allowed for degeneration since material was required for histological examination in connexion with another problem, and therefore the absence of spontaneous activity has little significance. In one rabbit the vagi were sectioned intra-abdominally and in two other animals the same procedure was performed in conjunction with a bilateral splanchnicotomy. In all three the slow *C* fibres persisted, as shown by velocity determinations of the components of the ascending mesenteric action potential and by the presence of an outcoming volley from the inferior mesenteric ganglion. In no instance was there the slightest indication of any spontaneous activity in the ascending mesenteric branches showing again that the slow *C* fibres do not enter the abdomen via the vagi.

Bilateral abdominal sympathectomy and splanchnicotomy

This proved particularly difficult until the time allowed for degeneration was reduced to 7 days. The procedure in no way reduced the size of the slow *C* fibre potential recorded from the ascending mesenteric nerve or that of the outcoming volley returning from the inferior mesenteric ganglion. Abdominal sympathectomy and splanchnicotomy cuts off the major part of the thoracolumbar outflow to the abdominal viscera, and it is extremely unlikely that the fibres come from the sacral autonomic. It therefore seems reasonable to assume that the slow *C* fibres are not autonomic efferents from the central nervous system. Certainty on this point could only be reached by showing the persistence of the slow *C* fibres after ventral root section from the level T4 to L3, a most drastic operation and certainly not feasible in the rabbit. The fibres

could be afferent with their cells in the dorsal root ganglia and this possibility may not be precluded by the results of the sympathectomy and splanchnicotomy since it has been stated that visceral afferents may reach the cord via somatic nerves. Since extensive dorsal root section is impracticable in the rabbit, a direct test of this point is lacking. Kuntz (1940) and Job & Lundberg (1952) have, however, reported the presence of fine *C* fibres whose cells lie in the peripheral nervous system of the cat, and it seemed reasonable to work on the assumption that the slow *C* fibres were their equivalent in the rabbit. Our attention was therefore directed to the periphery. The ascending mesenteric branches run very close to the superior mesenteric ganglion, and Langley & Anderson (1896) state that they 'join strands from the superior mesenteric ganglion, and give off filaments to the colon'. It was possible that the slow *C* fibres might form a system of internuncials between the superior and inferior mesenteric ganglia.

Solar ganglionectomy

A total of ten solar ganglionectomies were successfully completed. In one of these the slow *C* fibres had completely degenerated in the ascending mesenteric branches, and these latter showed the most marked spontaneous activity seen in the course of this work (Fig. 5). Fig. 6*a* shows the potential

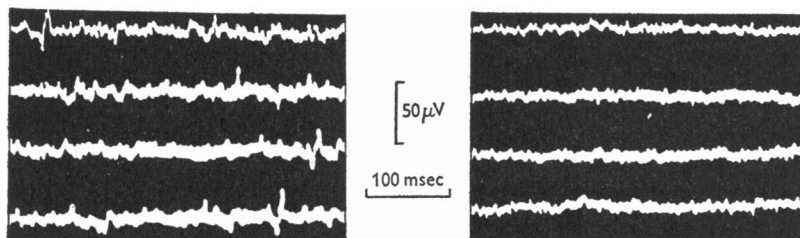


Fig. 5. On the left the spontaneous activity seen in the ascending mesenteric branches, and on the right the noise level of the recording system after the spontaneous discharge had been abolished by painting the ganglion with 0.1% nicotine acid tartrate. Solar ganglionectomy had been performed 7 days previously.

recorded by stimulating the ascending mesenteric branches and leading off between the stimulating electrodes and the ganglion. There is no sign of the action potential due to the slow *C* fibres or of the outcoming volley. Fig. 6*b* shows the action potential of the ascending mesenteric branches on stimulating an inferior splanchnic nerve. This response was abolished by painting the ganglion with 0.1% nicotine acid tartrate, showing that it was postsynaptic and not due to straight through fibres. The postganglionic neurones were therefore capable of being excited by preganglionic stimulation, so the absence of an outcoming volley from the ganglion when the ascending mesenteric branches were stimulated was confirmation that the slow *C* fibres had degenerated. In

the nine other experiments the outcoming volley from the ganglion persisted, but spontaneous activity in the postganglionic axons of the ascending mesenteric branches was observed in six out of eight instances where it was specifically looked for. The significance of spontaneous activity in this instance is doubtful since there may be preganglionic connexions between the solar and inferior mesenteric ganglia running in the intermesenteric nerves. Kuntz (1940), however states that 'most of the fibres of the intermesenteric nerves,

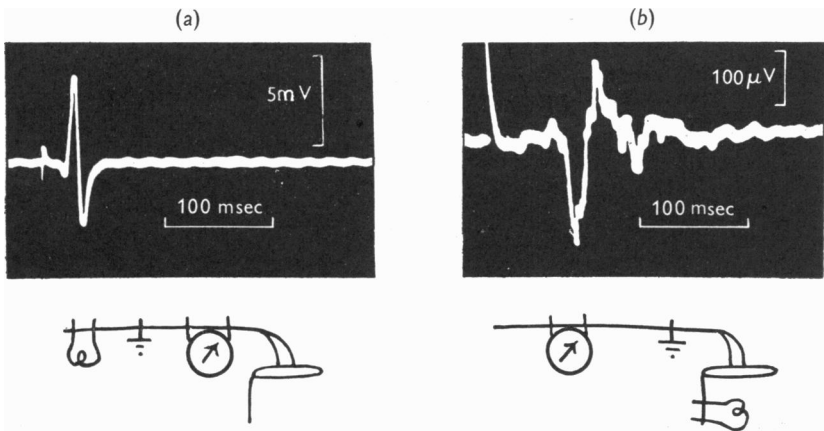


Fig. 6(a) Action potential obtained by stimulating and leading from the ascending mesenteric branches as shown in diagram below. Note absence of slow *C* fibre deflexion and of outcoming volley. (b) Action potential obtained by stimulating an inferior splanchnic nerve and leading from the ascending mesenteric branches. Same preparation as for Fig. 5.

except components of the lumbar splanchnic nerves, probably do not effect synaptic connexions in the inferior mesenteric ganglia'. It is probable therefore that in those instances where a spontaneous discharge from the ganglion was present, it was due to degeneration of the slow preganglionic fibres. Hence solar ganglionectomy probably interrupts some of the slow *C* fibres, but in only one rabbit was the interruption complete.

This would be expected if the fibres arose peripherally, came together on the superior mesenteric artery and then travelled caudally to the inferior mesenteric ganglion in the ascending mesenteric nerves. The extent of the removal of the slow *C* fibres would then depend on the length of the superior mesenteric artery that had been cleaned in the ganglionectomy. This idea was strengthened as a result of *in vivo* experiments. A pair of electrodes was placed on the ascending mesenteric branches just anterior to the inferior mesenteric ganglion, and the region of the superior mesenteric artery exposed by careful retraction of the viscera. Several strands of the nerve plexus surrounding this artery were placed separately on the recording electrodes and a maximal volley set up in the ascending mesenteric branches. In none of the

nerve strands which were seen to enter the superior mesenteric ganglion was there any sign of activity, whereas those which were distributed to the guts regularly showed small action potentials.

DISCUSSION

In spite of the equivocal nature of some of the evidence, it is possible to draw certain definite conclusions from these experiments. There is no doubt that the slow *C* fibres are anatomically quite distinct from the normal preganglionic fibres to the inferior mesenteric ganglion which have their cells in the lateral horns of the cord and travel from the lumbar sympathetic chains in the inferior splanchnic nerves. The cells of origin of the slow *C* fibres however lie somewhere on the headward distribution of the ascending mesenteric branches. The ascending mesenteric branches are chiefly composed of postganglionic fibres and form the main sympathetic supply to the colon. In a few experiments using balloon recording, stimulation of these branches produced an inhibition of the tonus and of the rhythmic contractions of the greater part of the colon thus confirming the views of Langley & Anderson (1896) on their distribution. It is not unreasonable as a working hypothesis, to assume that the slow *C* fibres originate in the colon possibly as axons of cells lying in the enteric plexus. This idea runs contrary to the plan of the autonomic nervous system so forcibly expounded by Gaskell (1916) and supported by Langley (1921). However, the work of the last thirty years has given numerous examples of exceptions to the general plan of these earlier workers, and to quote Mitchell (1953) 'the autonomic system is not the simple and primitive affair of some imaginations, and its subtleties of arrangement and function are still largely unfathomed'. Our experiments have produced no evidence contrary to the view of a peripheral origin of the slow *C* fibres. They definitely do not enter the abdomen in the vagi or the thoracic splanchnics, and degenerative section of these nerves, together with removal of the abdominal sympathetic chains leaves them intact. The first question to consider is: how completely does this procedure cut off the autonomic supply to the abdomen? The sacral outflow is still intact and forms a possible though unlikely path for the fibres, should their cells occupy the orthodox position of autonomic preganglionic nerve cells in the lateral horns of the spinal cord. There is evidence against this possibility from preliminary experiments performed to analyse the degree of overlap of the slow *C* fibres and the preganglionic fibres of the inferior splanchnics on the postganglionic neurones of the inferior mesenteric ganglion. Brown & Pascoe (1952) concluded that the degree of overlap, if it existed, was seldom extensive. This conclusion was reached from comparisons of the areas of the action potentials obtained by stimulating the two sets of preganglionic fibres separately and then together. This method is not conclusive, as was admitted by Brown & Pascoe, since occlusion will be obscured if, as is highly probable,

facilitation occurs concomitantly. Some experiments performed by one of us, jointly with Dr Lundberg, suggest that the degree of overlap is very extensive. This would hardly be expected if the slow *C* fibres arose from the sacral autonomic, since this would be an instance of the sympathetic and parasympathetic using a final common path.

There is little doubt that abdominal sympathectomy with splanchnicotomy cuts off the sympathetic efferent supply almost if not entirely, and vagotomy completely removes the cranial parasympathetic efferents. Certainty on this question would entail ventral root section which, as has been stated previously, is not a practicable procedure in rabbits. Unless the fibres enter the abdomen by some localized discrete and obscure pathway it is safe to conclude that they are not orthodox preganglionic autonomic axons. Various workers have reported efferent fibres leaving the cord in the dorsal roots, and although the work of Barron & Matthews (1935) shows that some of the myelinated fibres at least are collaterals of afferent fibres which have entered the cord through nearby roots, it is noteworthy that Mitchell (1953), in a recent review of the subject, considers that the anatomical and physiological evidence for dorsal root efferents outweighs that to the contrary. If the evidence for such fibres is doubtful, their peripheral distribution is more so, and the possibility that the slow *C* fibres are dorsal root efferents will be left until other more likely origins for these fibres have been eliminated. A more likely hypothesis is that the slow *C* fibres are collaterals of dorsal root afferents. This possibility is greatly reduced by the results of the extensive removal of the sympathetic and parasympathetic supply to the abdomen referred to above, but it cannot be completely eliminated, since visceral afferents are known which traverse somatic nerves. Kuntz (1940) and Job & Lundberg (1952) describe *C* fibres in the cat which do not come from the cord, but originate in the periphery and form synapses in the inferior mesenteric ganglion. Kuntz showed persistence of terminal networks in the inferior mesenteric ganglion after it had been chronically decentralized, and then demonstrated histologically that fine *C* fibres leave the colon in the colonic nerves. These fibres did not degenerate in the peripheral end of the nerve after it had been sectioned. Job & Lundberg, using electrophysiological methods, showed that the hypogastric nerves contained *C* fibres which formed synapses in the inferior mesenteric ganglion, and that these fibres did not degenerate after the ganglion was decentralized, nor after degenerative section of ventral and dorsal roots T11-L6.

These two sets of evidence from widely separate sources leave little doubt that preganglionic fibres originate from the periphery in the cat. The similar nature of the slow *C* fibres in the rabbit suggested to us that these also might arise outside the spinal cord. Since degenerative root section is not feasible in the rabbit, further work is in hand to ascertain if the slow *C* fibres leave the colon in the fine ramifications of the ascending mesenteric branches. A few

experiments have been performed to determine whether the fibres are sensory, forming the afferent side of a local reflex. These have not met with success possibly because the fibres are small in size and numbers relative to the mass of postganglionic fibres in the ascending mesenteric nerves. There is some evidence of a local reflex control of the gut via the inferior mesenteric ganglion; Garry (1933), for instance, speaking of the large bowel of the cat, states that 'division of the spinal rami to the inferior mesenteric ganglia alone certainly never causes such marked increase in colonic activity as division of the lumbar colonic nerves'. Lawson & Holt (1937) describe a similar effect in the dog, though since the ganglia were decentralized chronically in their experiments there exists the possibility that the local effects ascribed to the ganglia might have been due to spontaneous activity of the postganglionic neurones. Kuntz (1940) and Kuntz & Saccomanno (1944) claim that the intestino-intestinal reflex persists after chronic decentralization of the inferior mesenteric ganglion and removal of the lumbar sympathetic chains. The reflex is the name given to the inhibition of a proximal segment of gut when the pressure is raised in a distal segment. It is noteworthy that after the decentralization of the ganglion and removal of the sympathetic chains, Kuntz & Saccomanno found that a pressure of 200 cm of water was necessary to elicit the response, and that it could sometimes only be obtained once. This suggests that whatever the afferents were, they were not pressure receptors, but were stimulated and destroyed by the excessive distention. Freund & Sheehan (1943) showed clearly that the intestino-intestinal reflex, mediated through the coeliac ganglia, is abolished by sympathectomy from the stellate to the brim of the pelvis, but persists so long as one splanchnic or one lumbar sympathetic chain is intact. There is as yet therefore no evidence to suggest the function of the slow *C* fibres.

SUMMARY

1. Experiments have been performed on rabbits to determine the positions of the cell bodies of certain non-medullated nerves—the 'slow *C* fibres' which form synapses in the inferior mesenteric ganglion.

2. The origin of the slow *C* fibres has been investigated by means of degenerative section of visceral nerves; the final experiments were performed *in vitro*.

3. The cells of origin of the slow *C* fibres do not lie in the inferior mesenteric ganglion, nor do the fibres enter the abdominal cavity via the inferior splanchnic nerves.

4. The slow *C* fibres originate somewhere along the headward distribution of the ascending mesenteric branches but bilateral splanchnicotomy, alone or accompanied by bilateral vagotomy, or bilateral abdominal sympathectomy does not cause them to degenerate.

5. Solar ganglionectomy may cause degeneration of some of the slow *C* fibres.

6. It is suggested that the slow *C* fibres arise peripherally and possibly in the gut.

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