THE INTRAMURAL NERVOUS SYSTEM OF THE SMALL INTESTINE WITH SPECIAL REFERENCE TO THE INNERVATION OF THE INNER SUBDIVISION OF ITS CIRCULAR MUSCLE[1]

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In a previous communication (Li, 1936, 1937) it has been pointed out that the circular muscle of the small intestine of various vertebrates is subdivided into two layers, a thin inner layer and a thick outer layer. The inner layer is composed of one to several layers of muscle cells which are much smaller in size, sometimes branching and anastomosing with other muscle cells. This layer is richer in nuclei than the outer layer. Since it stands out as a separate entity and consists of a rather primitive type of smooth muscle cell, with occasional ganglion cells, it was suggested that it might be a "neuromuscular" structure and be responsible for irritability or conduction in the small gut. The present study deals with its nerve supply, a point of some importance in developing the neuromuscular idea.

PRESENT STATUS OF OUR KNOWLEDGE

Since very little is known about this subdivision of the circular muscle, nothing is to be found in the literature about its nerve supply. However, a general survey of our present knowledge of intestinal innervation will not be out of place, especially with a view to seeing how the special innervation of this particular layer fits into the general scheme.

The voluminous literature on this subject has been completely reviewed by Hill (1927), Schabadasch (1930) and Patzelt (1936). It is generally agreed that the small intestine, like other parts of the digestive tube, is supplied with nerves of extrinsic and intrinsic origin. Both vagus and sympathetic nerves enter the intestinal wall from without, but their mode of termination and their relationship to the intramural nervous system are not yet clear. According to Stoehr (1932) the intramural nerves of the intestine may be classified into four systems which are, however, very intimately connected: (1) plexus subserosus, which has been very well demonstrated by Schabadasch (1930); (2) plexus myentericus (Auerbach's plexus) lying between the circular and longitudinal muscle layers; (3) plexus muscularis profundus situated within the circular

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muscle (Drasch, 1881; Cajal, 1893); (4) plexus submucosus (Meissner's plexus) situated in the submucosa and extending into the mucosa. There are free anastomosing fibre strands between the myenteric and submucous plexuses.

The myenteric plexus consists essentially of three plexiform mesh works (Schabadasch, 1930; Stoehr, 1930; Greving, 1931), viz. a primary, a secondary and a tertiary plexus. The primary plexus is a relatively coarse structure. Its meshes vary within wide limits in size and form, but in general it exhibits a longitudinal arrangement. The secondary plexus is intimately connected with the primary but is made up of more slender bundles of nerve fibres. The primary and secondary plexuses lie mainly within the connective tissue between the circular and longitudinal muscle layers. The tertiary plexus is a very delicate meshwork of fibres directly connected with the secondary plexus, lying inside the circular muscle and running in the same direction. Its ramifications form a fine meshwork known as plexus muscularis profundus. According to van Esveld (1928*a*) this plexus is again divided into still finer meshes, the "plexus terminal ou interstitiel".

Meissner's plexus consists of several superimposed meshworks of nerve fibres and ganglia and has been described in the literature (Stoehr, 1930; Schabadasch, 1930) as composed of two plexuses, the plexus entericus internus (Henle's plexus) and plexus submucosus (i.e. the plexus submucosus in its narrow sense or Meissner's plexus proper). The plexus entericus internus is situated at the extreme periphery, that is close to the circular muscle. It differs considerably from the structure of Auerbach's plexus in the delicacy of its bundles and ganglia, as well as the irregularity in size and arrangements of its meshes. The plexus submucosus (in its narrow sense) is situated near the muscularis mucosae and is much finer in its meshes and elements than those of Henle's plexus.

It has long been known that in addition to the plexuses of Auerbach and Meissner and their nerve cells, there exists in the digestive tract another plexus consisting of anastomosing stellate and spindle-shaped cells with varicose processes. This "cell net" is often named the interstitial cell net of Cajal who first described it (Cajal, 1889, 1893). Uncertainty exists as to the nature of these interstitial cells and there are two contradictory views:

(1) *Nervous tissue view.* Cajal (1889) demonstrated the presence of a neurofibrillar network in these cells, varicosities on their processes and their deeply staining character with methylene blue. All these facts led Cajal and his pupil La Villa (1897) to consider them as nervous in character. Both of these authors failed, however, to demonstrate any connexion with extrinsic and intrinsic nerve fibres. P. Schulz (1895) and E. Mueller (1920) regard them as sympathetic nerve cells. Bethe (1903) and Prentiss (1904) consider them as a peripheral nerve cell net. Tiegs (1925) describes a nerve cell net of the gut wall (apparently identical with these cells) and he believes that it is the seat of the so-called myogenic contractions of the gut wall. Woollard (1926), in his study on the innervation of blood vessels, has observed a similar type of cell

net both in large and small vessels. He makes no comment on the nature of this cell net but emphasizes the fact that the large branching cells are closely related to the unmyelinated nerve fibres and that they persist after denervation by removal of the sympathetic trunk. Lawrentjew (1929) claims to have demonstrated nerve fibres in these cells and, upholding Held's theory, regards them as lemmoblasts. He considers the interstitial cell net as a syncytial structure, and holds that it functions as the end-part of a protoplasmic conducting tissue of the autonomic nervous system ("als Endglieder einer protoplasmatischen Leitungsbahn des autonomen Nervensystems"). This lemmoblastic concept has been well received by many authors (van Esveld, 1928*a*; Kolossow & Sabussow, 1928; Schabadasch, 1930; Stoehr, 1930) but not without modifications. Stoehr (1932) and his pupils (Reiser, 1933; Riegele, 1932) think that these interstitial cells are identical with the Schwann's cells and interpret them as the conducting tissue (Leitgewebe) or the conducting plasmodium (Leitplasmodium) of the peripheral nerve fibres. They consider this conducting tissue together with the nerve fibres embedded in its protoplasm as a nervous terminal plasmodium. Whether the cells can be considered as neurones is regarded as a question of minor importance. Schabadasch entertains the opinion that these cells may mean something more than a mere covering cell (lemmoblast) and be the generator of the neurofibrillae included in them. Boeke (1935*a*, *b*), while admitting the lemmoblastic theory, says that they may be comparable to the primitive ganglion cells of invertebrates as originally suggested by Cajal. Leeuwe (1937), working in Boeke's laboratory, has recently shown the ganglion cell nature of the interstitial cells with certainty. With methylene-blue staining he could trace syncytial connexions of these cells not only with the ordinary ganglion cells but also with all transitional forms between interstitial cells and ganglion cells. Within the cell body there is a neurofibrillar network which in his opinion is formed by the interstitial cell itself. Thus, the interstitial cells are true ganglion cells, and are not like lemmoblasts merely carrying fibres. Interstitial cells are usually well stained by intravital methylene blue, while Schwann's cells are not stained. Furthermore, they contain Nissl's granules which are stained with methyl green pyronin stain and thionin like ordinary ganglion cells. They show oxidase and peroxidase reactions similar to those in the ordinary ganglion cells. By staining for Reich's π-granules it has been made evident that they are distinct from lemmoblasts (Schwann's cells). In the intestine the varicose processes of the interstitial cells form a periterminal network around the muscle fibres and merge into their protoplasm. In a study of frog larva, he finds that they are genetically related to the sympathetic ganglion cells. Meyling (1938) not only supports Leeuwe's view but goes even one step further in putting forward the suggestion that the interstitial cells may be sensory or motor in character. According to him, sensory cells have thin, broad, lamellar, protoplasmic processes (comparable to the dendrite lamina of Lawrentjew (1929)), while motor cells have much narrower varicose protoplasmic processes.

(2) *Connective tissue view.* Dogiel (1895), being unable to find neurofibrillae in these cells or to trace any connexion between them and the nerve fibres of the enteric plexus, regards them as connective tissue cells. Huber (1897), Ebner (1889–1902), Heidenhain (1911), Kuntz (1922), Tello (1922), Johnson (1925) and Oshima (1929) all fail to find neurofibrillae in these cells, and accordingly support Dogiel's view that they are some peculiar type of connective tissue cell. Thus the arguments for this view are based mainly on negative findings.

It seems that positive facts are accumulating in favour of the view that the interstitial cells are primitive ganglion cells and that they are an important constituent of the enteric nervous system.

MATERIAL AND METHODS

The small intestine of rabbit, guinea-pig, cat and dog was studied by the intravital methylene-blue and the Gros-Bielschowsky stain.

Intravital methylene-blue stain

The animal was killed by a blow on its head, and its blood was washed out with 0·72 % NaCl solution through the thoracic aorta. When the outflow from the inferior vena cava became clear, methylene-blue solution was substituted. The staining solution was made up as follows: methylene-blue 0·25–0·33 g., sodium chloride 7·2 g., distilled water 1000 c.c. The distilled water was first boiled to 100° C. to expel the carbon dioxide and then cooled down to 37° C. Gurr's methylene-blue "medicinal" proved satisfactory. I found that the addition of 0·2–0·3 g. of resorcin to each litre of the dye quickens the process of staining as described by Schabadasch (1935). For the guinea-pig 1000–1500 c.c., for the rabbit and cat 2000–3000 c.c. of the dye were used. After the injection the abdominal cavity was opened and the intestine exposed to the air. Within 10 min. the nerve plexuses were intensely blue, standing out clearly. The intestine was then taken out and fixed in 5–8 % solution of ammonium molybdate.

Spreads were prepared from the well-fixed tissue by separating different layers of its coats. The specimens were mounted in sandarac in eucalyptus oil. I am grateful to Prof. J. P. Hill for this method. The preparation is brought from water to 70 % alcohol, to acetone 3 parts plus eucalyptus oil 1 part, to pure eucalyptus oil and finally mounted in sandarac in eucalyptus oil. Dioxan was also tried—from water to two changes of dioxan, then to oil, and mount in sandarac. These methods prove very satisfactory because the decolorization and shrinkage caused by alcohol and xylol are avoided. For paraffin sections I used dioxan for dehydration and clearing before embedding, as methylene-blue is barely soluble in dioxan.

Gros-Bielschowsky's method

Both Denny-Brown and Richardson's modification were used after fixation in 10% formol plus 2% pyridine, 20% neutral formalin and Lawrentjew's A.-F.-A. mixture. Frozen tangential and transverse sections of cat's and dog's intestine were stained with silver and counterstained with Ehrlich's haematoxylin and eosin. Strips of rabbit's intestine were also stained in the same way. Strips of the longitudinal muscle were easily stained, while the circular muscle and submucosa very seldom gave satisfactory results because of a too dark background. Lawrentjew's fixing mixture followed by silver was specially valuable for the interstitial cells of Cajal.

OBSERVATIONS

On the inner layer of the circular muscle

In flat silver preparations of rabbit's and guinea-pig's small intestine, Meissner's plexus does not appear to be divided into Henle's plexus and Meissner's plexus proper. It is closely applied to the inner layer of the circular muscle, and is composed of interlacing nerve-fibre bundles which are thinner than the fibre strands of Auerbach's plexus. The shape of the meshes may be triangular, quadrangular or polygonal. The ganglia are usually found at the intersections of its anastomosing branches, and are either fusiform or triangular. They contain only a few ganglion cells.

Thick fibre bundles of this plexus send off thinner fibre strands which run mainly in the direction of the circular muscle fibres and anastomose among themselves. The nerve fibres are accompanied by cells and form finely reticulated structures similar to the sympathetic ground plexus of Boeke and the terminal reticulum of Stoehr. Individual nerve fibres have never been noticed leaving a fibre strand to supply the muscle fibres directly. The reticular network is, however, closely associated with the interstitial cell of Cajal. The interstitial cell not infrequently has a process inside the reticulum, taking part in the formation of this fine network. Other processes of the interstitial cells anastomose freely with each other. Some of them seem to end in close relation to the muscle fibres, but the mode of ending cannot be determined.

In methylene-blue flat preparations of the circular muscle, numerous nerve fibres are found within its inner layer in addition to the branches of the overlying Meissner's plexus. Surrounding nearly every muscle fibre there are nerve fibres. Most of them are smooth but slightly wavy, taking a more or less straight course along the muscle fibres. Some of them are definitely varicose. They branch infrequently and anastomose among themselves. These fibres are of local origin; they are the protoplasmic processes of a type of interstitial cell of Cajal. The cells are mostly spindle-shaped and bipolar, less frequently tripolar or multipolar. The cell body is stained less deeply with methylene-blue than the interstitial cells attached to the longitudinal muscle to be described later. The whole picture resembles what Schabadasch (1930) described as the *plexus muscularis profundus*. Schabadasch places this plexus between the circular and longitudinal muscle layers in the colon, but I believe it to be in the inner layer of the circular muscle of the small intestine. This observation on flat preparations is confirmed in paraffin sections. Both in transverse and longitudinal sections the inner layer of the circular muscle stands out as a blue band because of its richness in nerve fibres and interstitial cells, both of which stain blue.

In silver preparations of cat's intestine, the inner layer of the circular muscle is almost stained black in contrast with the outer layer which remains colourless. There is a fine meshwork which is formed by the anastomosing protoplasmic processes of stellate cells. Fine deeply stained black fibrils (apparently nerve fibres) are sometimes found within the stellate cells. Some of these fibres can be traced back into Meissner's plexus. In tangential sections where this layer is caught in big sheets (Pl. I, fig. 1), one is impressed by the fact that this inner layer contains many more nuclei than the outer layer. The anastomosing cell net is better seen. The stellate cells have a small amount of cytoplasm with oval nuclei devoid of nucleoli. The nuclei are mostly arranged in the direction of muscle fibres, and the anastomosing processes are rather broad and lamellar in appearance. At first glance these cells are not dissimilar to the connective tissue cells found in the boundary zone between the submucosa and the circular muscle by van Esveld (1928*a*, Abb. 18), but C. J. Hill agrees with me that they are interstitial cells. Through the kind introduction of Prof. Hill, I have recently had the opportunity of showing Prof. Boeke my preparations, and he remarked on the similarity of these cells to the interstitial cells described by Meyling (1938) in connexion with the carotid sinus. Their nervous nature can hardly be doubted when one admits that the interstitial cell is a primitive type of ganglion cell (Boeke, 1935 *a*, *b*; Leeuwe, 1937). Fine fibrils are sometimes seen inside this protoplasmic network. They seem to be of local origin and produced by the interstitial cells. Nerve fibres from Meissner's plexus are frequently traced into this layer forming a separate network but closely related to the interstitial cells. The relationship may be best expressed by Prof. Woollard's (1926) description of the nerve supply of blood vessels: "These cells vary in form and seem sometimes to be in apposition with the naked axis cylinder; again they appear to be at the end of a naked cylinder as though this was inserted into the cell; often they appear to be more independent of the axis cylinder. They are characterized by giving off complicated processes which entwine with the axis cylinder." It is a striking fact that definite nerve endings have not been observed. In the dog's intestine a similar black-staining network is present in this layer, but the protoplasmic processes are not so broad. The cells are bipolar, tripolar or, less frequently, multipolar, and are quite typical of interstitial cells.

Outer layer of circular muscle

In methylene-blue preparations of rabbit and guinea-pig intestine (longitudinal and outer circular muscle coats together) which we viewed from the serosa side, strands of nerve bundles of different calibre can be seen forming the primary, secondary and tertiary plexuses described by Schabadasch (1930). Nerve strands of the tertiary plexus run in the outer layer of the circular muscle and mainly in the direction of the muscle fibres. In the interstices of the tertiary plexus there is a loose network of the interstitial cells of Cajal. Protoplasmic processes of the interstitial cells join the finest fibre strands of the tertiary plexus as well as the feltwork of interstitial cells between the circular and longitudinal muscle layers. A few of the varicose processes seem to end in relation to the muscle fibres as end-knobs. Whether these are the actual endings or the torn ends of the processes or partially stained processes cannot be decided.

Longitudinal muscle layer

In stripped preparations Auerbach's plexus is usually attached to the inner surface of the longitudinal muscle coat. There is also a dense feltwork of interstitial cells of Cajal. These form a sheath to the nerve strands of Auerbach's plexus; their protoplasmic processes contribute to the bulk of the nerve strands. Between the meshes of Auerbach's plexus the interstitial cells form a continuous network. Fibre strands from the nerve trunks are frequently seen connected with the meshwork of interstitial cells; in other words, the fibres of the interstitial cells enter into the composition of the fine nerve-fibre strands. The cell bodies are as a rule arranged in the direction of the longitudinal muscle fibres. The whole picture of this feltwork (Pl. I, fig. 2) reminds one of the subserous plexus of Schabadasch (1930) in spite of the topographical discrepancy. His plexus is located in the subserosa (i.e. on the outer surface of the longitudinal muscle), and is composed of anastomosing interstitial cells. He described nerve endings passing from this plexus to the longitudinal muscle. I have found no plexus of a similar type in the subserosa.

Morphology of the interstitial cells and their relationship to the fibre strands and ganglion cells of Auerbach's plexus and the muscle cells

The interstitial cells (Pl. I, fig. 2, and Pl. II, figs. 3, 4) are best seen in the flat preparation of the longitudinal muscle of specimens stained by the intravital methylene-blue and the silver impregnation methods. Morphologically they conform to the description of Hill (1927), van Esveld (1928*a*) and Schabadasch (1930). They are stellate or spindle-shaped cells with two to five protoplasmic processes without any differentiation into axon and dendrites. The processes are usually very long and branching and anastomosing among themselves. Sometimes a side branch is seen to end in the muscle as a varicose swelling, in the manner shown by van Esveld (1928*a*, Abb. 16). Endings are, however, very infrequently seen. These processes give different pictures in methylene-blue and silver preparations. In methylene-blue stained specimens they usually show numerous varicosities and are indistinguishable from the varicose processes of the ganglion cells. In silver specimens there is no sign of varicosity and they look like the ordinary nerve fibres in spite of their thick calibre. At the bifurcation there is a triangular knot which gives the typical picture of Remak's knot of nerve fibres. Unless they are traced to the cell body, it is almost impossible to distinguish fibres of interstitial cells and those of the true ganglion cells. I have seen not infrequently in methylene-blue preparations nerve fibres with alternate smooth and varicose segments. The cell body contains comparatively little cytoplasm in which there are granules staining deep blue with methylene-blue. The nuclei are oval in shape, devoid of nucleoli, and deeply stained with silver.

Between the fibre strands and the ganglion cells of Auerbach's plexus and the interstitial cells, a definite relationship exists. The interstitial cells form a dense network around the trunks of nerve strands of Auerbach's plexus. The fibres of the interstitial cells enter the fine fibre strands of the Auerbach's plexus; very frequently one sees that the fine fibre strands break into individual fibres which anastomose with those of the interstitial cells. In Pl. II, fig. 3, are shown the processes of a ganglion cell and interstitial cells forming a loose network where synaptic connexions may occur. Fibres of the interstitial cells form an interlacing network within the fibre strands and around ganglia of the Auerbach's plexus (Pl. II, fig. 4). It is highly probable that synaptic connexions between the two cell systems may occur there.

DISCUSSION

The inner layer of the circular muscle is especially rich in nerve fibres, some of which can be traced to Meissner's plexus. They form a fine meshwork and seem to end here with the intervention of the interstitial cells. The majority of the fibres in this layer are, however, of local origin. They are the protoplasmic processes of interstitial cells of Cajal. They stain with methylene-blue and silver. They are smooth or varicose, or slightly wavy, running a parallel course with the muscle fibres. They differ from elastic and reticular fibres, which are also numerous in this layer, in their staining properties and their arrangement. The elastic fibres in this layer form a dense network which is the continuation of the elastic network in the submucosa. The reticulum runs parallel to the muscle cells but gives off numerous side branches to embrace the muscle cells. The interstitial cells giving rise to fibres appear to me to be more primitive than the interstitial cells in the outer coat which are discussed later. They are usually bipolar, less frequently tripolar and multipolar, and contain fewer granules stainable with methylene-blue. Their processes are rather smooth and less varicose. All of these facts are in favour of the suggestion that they are very primitive.

This plexus of interstitial cells seems to have very little connexion with Auerbach's and Meissner's plexuses but is more closely related to the interstitial cells in the neighbourhood. By means of their protoplasmic processes a connexion is established with interstitial cells in the submucosa and the outer layer of the circular muscle. Furthermore, they communicate with the dense interstitial cell net between the circular and longitudinal muscles at the place where the inner layer of the circular muscle dips down.

Both in the rabbit's and guinea-pig's intestine, where the inner layer of the circular muscle is thin, the interstitial cells and their fibres form a plexus which recalls the picture given by Schabadasch of plexus muscularis profundus in spite of the topographical difference. This author did not state clearly the origin of the fibres of this plexus.

In the cat's and the dog's intestine, where the inner layer of the circular muscle is thick, there is a dense network of interstitial cells, but the picture is somewhat different. In the dog's intestine the interstitial cell net in this layer contains bipolar as well as tripolar and multipolar cells. In the cat's intestine the interstitial cell net in this layer resembles the interstitial cells described by Meyling in the carotid sinus. The anastomosing protoplasmic processes are thin, but broad and lamellar. It is interesting to note that Meyling's sensory interstitial cell net of the carotid sinus is embedded between the elastic fibres. It may be pointed out that the inner layer of the circular muscle is also especially rich in elastic fibres.

The outer layer of the circular muscle and the longitudinal muscle of the small intestine are supplied by branches of Auerbach's plexus through the mediation of interstitial cells of Cajal. These form a very dense network in the space between the circular and longitudinal muscle layers, where Auerbach's plexus is located. They constitute a sheath to the primary and secondary plexuses of Auerbach and enter into the composition of the nerve strands. They also show definite connexions with the ganglion cells as enumerated in the previous section. The interstitial cells in this place extend into the circular and longitudinal muscles where they are connected with the finest branches of Auerbach's plexus, and supply occasional endings to the muscle. Thus together with the tertiary nerve fibres of Auerbach's plexus they form the "plexus terminal ou interstitiel" of van Esveld.

The interstitial cells are well developed here. They are mostly multipolar cells with narrow varicose processes and without differentiation into axon and dendrites. The cell body contains granules deeply stained with methylene-blue. They belong morphologically to the group of motor interstitial cells of Meyling.

My present study reveals two types of interstitial cell net: (1) located in the inner layer of the circular muscle and composed of rather primitive interstitial cells, and (2) located between the circular and longitudinal muscles and within the outer layer of the circular, composed of well-developed interstitial cells. Judging from my own observations and the facts presented by others, there seems to be no doubt about their nervous character, and that they are a primitive type of ganglion cell. I am not in a position to say whether they can be divided into sensory and motor types. It seems to me this classification is unnecessary because not infrequently in the lower animals the primitive ganglion cells have both sensory and motor functions.

Since the inner layer of the circular muscle contains an abundance of interstitial cells which are considered as primitive nerve cells, this layer of muscle may be regarded as a neuromuscular structure.

I am in agreement, therefore, with Catel (1936) that the intestinal innervation is effected through three systems: (1) extrinsic nerves, i.e. vagus and sympathetic, (2) intramural ganglion cell systems composed of Auerbach's and Meissner's plexuses, and (3) the interstitial cells of Cajal. The first exerts a dominating influence over the other two. The last is considered as the end-part of the enteric system and is capable of carrying out the ordinary activity of the gut in the absence of the ruling influence of the other two as shown by van Esveld in ganglion-cell-free muscle preparations with physiological methods (1928*b*). That the intestinal tract maintains a primitive type of nervous organization is to be expected, since its impulses, as well as its motor activities, only involve a very simple type of nervous action. Even its rate of conduction is similar to the primitive ganglionic plexus of coelenterates (20 cm. per sec., Alvarez, 1922) and the current may run in both directions.

SUMMARY

1. The circular muscle of the small intestine of many vertebrates consists of a thick external and a thin inner layer.

2. The external layer is supplied by the tertiary branches of Auerbach's plexus and a cell net of well-developed interstitial cells of Cajal, comprising the "plexus terminal ou interstitiel" of van Esveld.

3. The inner layer is specially rich in nerve fibres which are mainly of local origin, being the protoplasmic processes of a rather primitive type of interstitial cell of Cajal.

4. The interstitial cells of Cajal are well developed in the space between the circular and longitudinal muscles and in the external layer of the circular muscle. Definite relationships between the interstitial cells, the nerve fibre strands and the ganglion cells of Auerbach's plexus, and the muscle cells are emphasized.

5. The interstitial cells of Cajal are in all probability primitive ganglion cells as suggested by Cajal, Boeke and Leeuwe.

6. Since the inner layer of the circular muscle is rich in primitive nervous elements, it may be considered as neuromuscular in nature and may have definite relations to irritability, conduction and rhythmic contractions.

7. Catel's hypothesis of intestinal innervation receives support from these observations.

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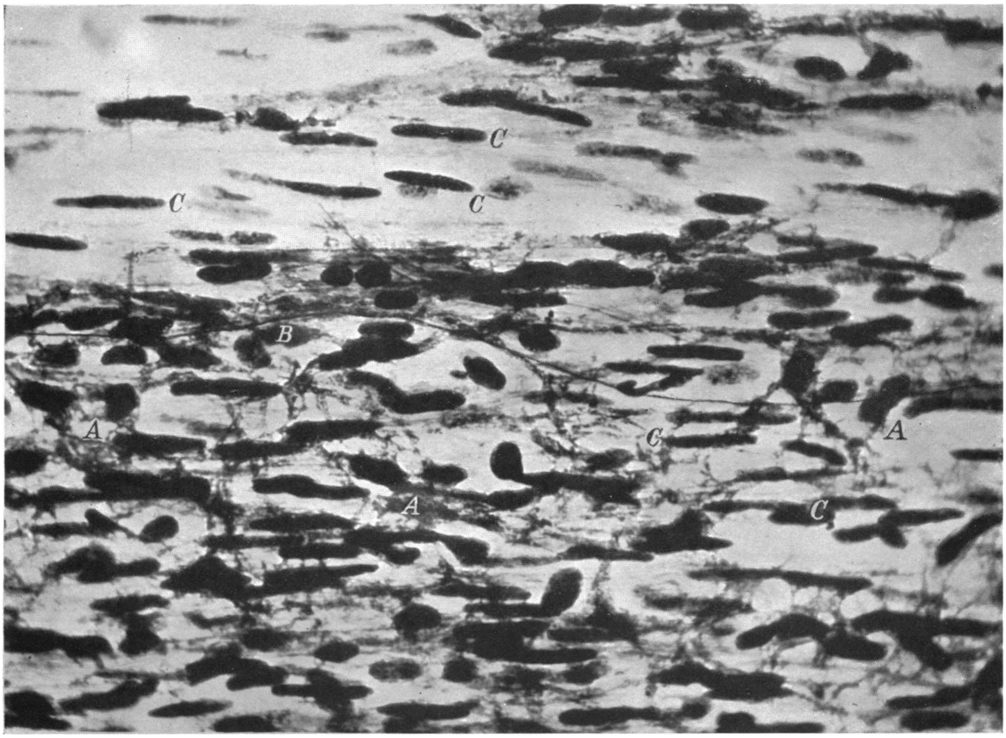

Fig. 1.

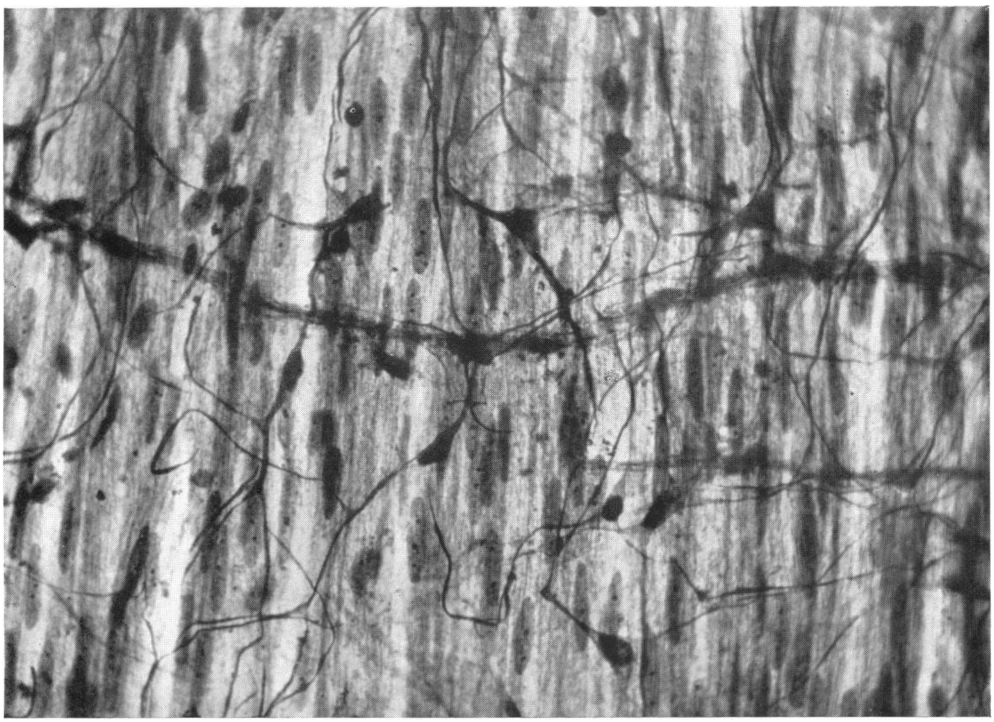

Fig. 2.

PEI-LIN LI—INTRAMURAL NERVOUS SYSTEM OF THE SMALL INTESTINE.

Fig. 4.

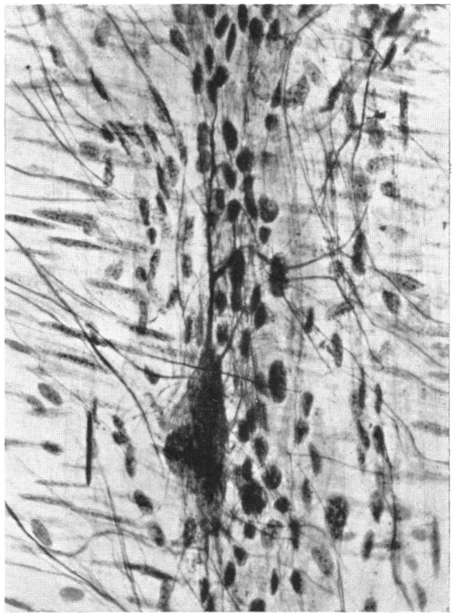

Fig. 6.

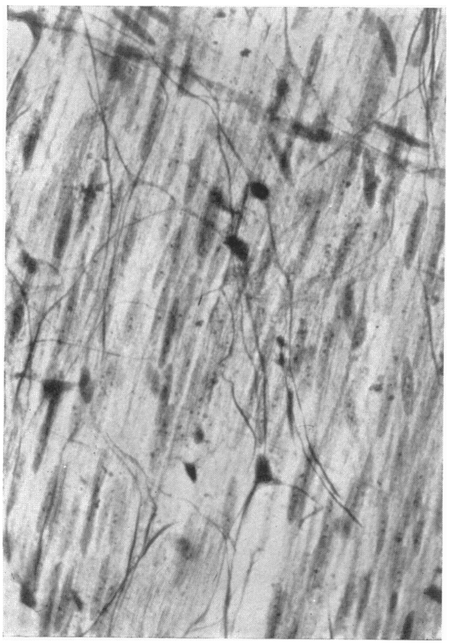

Fig. 3.

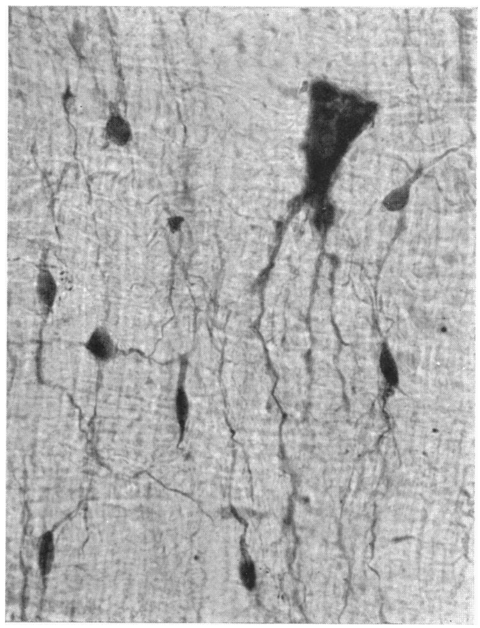

Fig. 5.

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EXPLANATION OF PLATES I AND II

PLATE I

Fig. 1. Tangential section of cat's small intestine stained by Gros-Bielschowsky method, showing interstitial cell net in the inner layer of circular muscle. The outer layer of circular muscle is clear. A, interstitial cells; B, nerve fibre; C, muscle nuclei.

Fig. 2. Rabbit's small intestine showing the interstitial cell net on the longitudinal muscle. Notice the Remak's knots at the bifurcation of fibres.

PLATE II

Fig. 3. Showing the processes of a ganglion cell and interstitial cells forming a loose network where synaptic connexions may occur. (Methylene-blue preparation.)

Fig. 4. Showing the cell body and varicotic process of an interstitial cell. (Methylene-blue preparation.)

Fig. 5. A methylene-blue preparation of longitudinal muscle showing the entwining of processes of interstitial cells and a ganglion cell.

Fig. 6. Silver preparation of longitudinal muscle of rabbit's small intestine showing the fibres of interstitial cells within and around the ganglia of Auerbach's plexus.