Organization of the muscular wall of the human colon

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The colon is the portion of the alimentary tract that has generated least interest among investigators and although the last decade has seen new methods applied to physiological problems in the large bowel, the detailed anatomy of the muscular layer remains a neglected subject, with the successfully located articles which consider this matter very few in number.

Each of us undertook an independent investigation and in this field of pattern recognition where observer error can be very gross, our conclusions have been surprisingly similar, so much so that a common set of photographs serves to illustrate the results.

MATERIALS AND METHODS

An independent investigation was carried out by each of us using similar methods but on different material.

In the first series (J.L.P.), postmortem specimens were used and included only colons removed from patients who had died of conditions unrelated to colonic disease. The colons were obtained within 12 to 24 hours of death, and were left in 10% formol saline for not less than 24 hours or in Carnoy's fluid for a few hours. Some were fixed in distension and others undistended. Portions from the different regions of the colon, some including a taenia and others from the intertaenial wall, were examined. Small pieces (about 5×5 cm) were removed and the serosa, mucosa, and submucosa dissected away. More than 30 specimens were examined. Portions of the colonic wall (12 specimens) were also treated enzymatically before dissection using Carnoy-fixed material, by incubation at 37°C for 16 hours in a 1 mg/ml collagenase solution in normal saline. This technique removes the connective tissue from between the fasciculi, which were thus rendered looser and easier to follow.

The second series (I.W.), was confined to operative specimens placed in formol saline within two hours of removal. After a variable fixation period, usually several weeks, small pieces (about 8×6 cm) containing a taenia were cut from apparently normal areas of colon and examined under a dissecting microscope after the mucosa or serosa had been stripped away. More than 100 pieces were examined, 60 from the sigmoid, usually fixed flat under tension by a technique for assessment of carcinoma of the rectum (Dukes and Bussey, 1958), 20 from the ¹Present address: Newmarket General Hospital, Suffolk.

ascending colon, and 20 from the transverse colon. All areas, including the three taeniae, were examined at some time both distended and opened before fixation. Those specimens with visible diverticula were excluded, but in view of the age of the patients who have part of the colon removed for neoplasm, and these were the bulk, it is likely that some examples of diverticular disease escaped detection (Williams, 1967). No muscle was obviously hypertrophied, but here again the impossibility of diagnosis of this in life, lack of knowledge of how long it takes to regress after a colostomy, and the great difficulty of diagnosing it in the specimen, means that a few examples may have gone undetected. It is an account of the mature and ageing colon.

In a separate group of nine cases, adjacent portions of the same normal sigmoid colon were fixed either distended at an unmeasured pressure or left free to contract in the fixative. These were compared with dissection and histological section.

RESULTS

CIRCULAR MUSCLE Under the dissecting microscope, when the longitudinal layer has been removed, it is immediately apparent that the circular muscle is not a uniform sheet, but is completely divided into 'bands' by connective tissue clefts (Figs 2a and b) penetrating the whole thickness of the muscle. The clefts, represented on the surface by superficial grooves (Fig. 1), are circumferential and parallel and extend for a variable distance, but rarely completing a single intertaenial segment. They contain loose connective tissue though often a distinct septum can be recognized within (Fig. 3). The width of these bands, which are continuous under the taeniae (Fig. 1), is variable but mostly within the range of $\frac{1}{2}$ to $1\frac{1}{2}$ mm, with the majority near 1 mm. They divide unequally, the divisions anastomosing with other bands, or with other divisions to form new bands, with a distance of some 1 to 4 cm between the branchings (Figs 1, 2a, and 2b).

Closer inspection of the bands show them divisible into smaller units, the 'fasciculi', four to six to each band being a common finding. At microdissection of formalin-fixed specimens, the fasciculi sometimes fall apart quite easily, but when any pressure is used





FIG. 2a.

FIG. 2b.



FIG. 3.



FIG. 4a.

FIG. 1. The outside of the sigmoid colon with the serosa removed. The taenia (A) has a grooved surface, while the fainter grooves in the intertaenial region (B) delineate its banded structure. Where the longitudinal muscle has been removed (C) the circular muscle banded meshwork can be seen continuous under the taenia.

FIG. 2 Circular muscle from the contracted colon with the longitudinal layer and submucosa removed (a). On the left the expanding meshwork is seen undisturbed but with traction on the right the unequal dividing of the bands becomes apparent. Circular muscle from the distended transverse colon (b). The fasciculi into which the bands divide are clearly visible.

FIG. 3. Longitudinal section of transverse colon. There are some six bands in this section varying in width from $\frac{1}{4}$ to 1 mm. Between them are gaps through the whole depth of circular muscle, most containing an obvious collagen septum. The inner half of each band shows the division into fasciculi but the outer half appears more solid. (Iron haematoxylin and van Gieson.)



FIG. 4b.

FIG. 4. A transverse section of the mesenteric taenia in a contracted sigmoid colon with Auerbach's plexus marking the division between the two muscle layers (a). Most of the surface grooves penetrate only halfway through the thickness of the taenia. Below, at this magnification the muscle appears solid. Transverse section of the anterior taenia of contracted mid transverse colon (b). In the outer part of the taenia (A) the muscle fibres are separated by septa to form a banded structure, but in the inner part (B) they show a mosaic pattern; (C) indicates the circular layer.





FIG. 5. The expanding network for the circular muscle of the sigmoid colon. Originally the taenia above was attached to, and the same length as, the circular muscle below. With this degree of elongation the bands move apart to show the expanding mesh arrangement (the taenia is about 1 cm in width).

FIG. 6. Lineback's view of the interconnexions of the two layers. At (a) the circular fibres interdigitate with the underside of the taenia. At (b) taenial bundles of a size visible to the naked eye turn at right angles to pass into the circular layer. For points (c) and (d) see text. Reproduced by courtesy of the Editor of the American Journal of Anatomy, from Fig. 22 of Lineback (1925).

FIG. 7. Longitudinal section to show muscular interconnexions (A) between the longitudinal (B) and circular (C) muscle layers at the site of the taenia. Note the close relationship to the mesenteric ganglia (D) (Mallory).

FIG. 8a. Intertaenial longitudinal sections of adjacent areas of the same sigmoid fixed contracted (1) and distended (2). Note that the bands become about half the height, are clearly separated from each other, and their mucosal ends are rounded in distension (van Gieson). (To same scale.)

FIG. 8b. Intertaenial longitudinal sections of contracted and distended sections cut from the same histological block. The circular muscle in distension is about one third the depth of the contracted state, and the gaps between the bands are wider. Fasciculation is very prominent in this specimen (van Gieson).



fig. 8b.

FIG. 5.



FIG. 7.



FIG. 8a.



FIG. 9. Transverse sections of adjacent portions of the same sigmoid, on the left fixed contracted and on the right distended. In distension the surface grooves on the taenia are wider (A) and reach almost to the circular layer, while the intertaenial muscle (B) is reduced to a thin, widely spaced banded layer.

dissection artefacts appear, and it is a simple matter to demonstrate the organization in which one believes. Nevertheless, both of us are convinced that there are fasciculi between 50 and 200 μ in width, with many near 100 μ . They can be distinguished in longitudinal histological section (Fig. 3) where they give the inner end of the band a fronded border. Complete connective tissue septa are not found between individual fasciculi, which are more difficult to distinguish histologically in the outer half of the band.

Although it is possible to dissect out a thin layer of muscle in the shape of a spiral of two to three turns around the circumference and thus to parallel the account of Goerttler (1932) for small intestine, both of us eventually concluded that the fasciculi were so interconnected that it would be unwise to give a measured length to a particular fasciculus. Attempts to describe a substructure for the fasciculus were soon abandoned because of the same uncertainty about technical artefacts.

The muscle of the bands then, though divisible into fasciculi, remains as an interconnected unit. The main conclusion is that the circular muscle is organized into an expanding meshwork of inter-3 connected bands most clearly seen in these formalinfixed specimens under tension (Figs 2a and 5).

LONGITUDINAL MUSCLE Longitudinal muscle covers the whole colon as a complete coat. In the intertaenial areas it forms a thin layer of cells again aggregated into a banded arrangement. This is very apparent in the sigmoid under the dissecting microscope (Fig. 1) and histologically (Fig. 9). Interconnexions between the bands have been recognized with moderate frequency but their demonstration is much more difficult than in circular muscle. In distension the bands move apart leaving gaps easily seen in transverse histological section (Fig. 9). The recognition of this layer in longitudinal histological sections will depend on whether the cut lies between or along a band, while a slightly oblique crossing will give the appearance commonly described as a patchy longitudinal coat. We both believe this to be a regular organized system of bands with gaps or potential gaps between them and not randomly arranged groups of cells.

The muscle of the taeniae is tougher and contains more connective tissue, so that attempts to dissect it lead to tearing. The taeniae are continuous with the intertaenial longitudinal muscle, arising by a gradual increase in thickness so that on close inspection they do not have a sharp edge, except where they cross an interhaustral cleft. Here the border is quite sharp and a small recess extends under the free edge of the taenia. The outer surface is marked by grooves (Fig. 1) which vary in their conspicuousness (Figs 4a and 4b) and contain connective tissue partitions dividing the outer part of the muscle into bands, but in contradistinction to the circular muscle these septa rarely penetrate the whole thickness of the layer. The bands join and anastomose with each other, but in the deeper layers there is no clear-cut banded structure. The reason is best seen in histological section where minor connective tissue septa run at all angles dividing the muscle into a mosaic of cell groups (Fig. 4).

CONNEXIONS BETWEEN THE LONGITUDINAL AND CIRCULAR LAYERS Both of us expected to confirm the results of Lineback (1925) who draws discrete bundles of cells of considerable size (1 to 2 mm width) passing from the underside of the taeniae to turn at right angles to join the circular layer (Fig. 6). In no case could this arrangement be seen under the dissecting microscope, even after the use of techniques to digest connective tissue. Both series found a firmer attachment of the circular muscle to the edge of a taenia than at its central portion. Both of us agree that there are interconnexions of muscle between the layers, of a size recognizable at histological section (Fig. 7), and a firm collagen binding. One of us (Pace, 1966, 1967, 1968), with the benefit of more extensive histological examinations, is of the opinion that these interconnexions are organized in pattern, and describes them in separate publications.

THE MUSCLE IN DISTENSION AND CONTRACTION A short study of the human sigmoid colon in distension and contraction was undertaken by one of us (I.W.), when the lumen of the muscular wall was commonly found to be twice the diameter and originally equal lengths about twice as long in distension as in contraction. Thus the structures in 1 sq cm in contraction are spread over 3 to 5 sq cm in distension, producing striking visual effects.

The circular muscle cut from blocks judged by eye to lie in the axial plane of the bowel was from two to three times thicker in contraction (Figs 8a and 8b). There was commonly a change in shape of the bands, the inner edge becoming smooth and rounded in distension (Fig. 8b), and the fasciculi usually but not always less obvious. In marked distension the bands could be clearly seen to be separated (Fig. 8), but did not themselves noticeably widen.

The intertaenial longitudinal muscle in transverse section changed from easily-seen thick bands in contraction to flatter, widely spaced bands in distension (Fig. 9). The taeniae, noticeably thinner in distension, tapered into the intertaenial muscle more gradually so that the edges became less distinct. The mosaic portion of the inner half was thinner and less obvious allowing the collagen septa to approach the circular layer (Fig. 9).

The smooth muscle cell nuclei are shorter and fatter in contraction, but considerable variation was seen in any one layer of any histological section. In distension Auerbach's plexus is much less obvious, and may even be flatter in shape, than in the contracted state.

FIXATION MUSCLES These, fully described by Fujita (1952), are tags of muscle arising in the muscular layers of the colon to run outwards at right angles to the lumen, inserting into the parietal wall. An occasional example was recognized in the second series of specimens but none was studied.

DISCUSSION

A CORRELATION WITH THE WORK OF OTHERS The present investigation deals with the anatomy of colonic muscle as seen at microdissection level only. Detailed histological studies are described elsewhere (Pace, 1966, 1968).

Lowitz (1896) observed that the muscle of the colon consists of fasciculi, Lineback (1925) described the nature of these fasciculi and their behaviour in dilatation and contraction, and Austoni (1937) gave a detailed account of the taeniae describing their arrangement into fasciculi and bundles. The present findings confirm, but elaborate somewhat, the observations of these investigators. In this connexion it should be noted that the term 'band' used in this paper corresponds to the term 'bundle' and 'fasciculus' used by these investigators, though Austoni subdivides his bundles into fasciculi. Lineback's small bundle or subfasciculus corresponds to our term 'fasciculus'.

The circular muscle was described by Lowitz (1896) as being thicker at the taeniae than in the wall between, in contrast to Lineback (1925) who believed that the circular muscle showed marked thinning beneath the taeniae. It is possible that groups of muscle cells, which at the borders of the taeniae change direction from longitudinal to circular, could somewhat augment the circular muscle layer in the intertaenial zone and so account for this layer being thinner beneath the taeniae than in between.

The continuity of the longitudinal muscle in the intertaenial area still seems to be a matter of controversy. The results of the present investigation show that at all ages and in all regions of the colon the outer longitudinal coat is continuous between the taeniae, though in distension gaps can occur between the bands.

The main result of this work, and where it differs from previous investigations, is the concept of an expandable meshwork into which both muscle layers are organized and which completely encircles the colon throughout its whole length. Such an expandable network adapts the circular muscle to an increase in length of the colon while preserving mechanical strength and a functional organization.

Lowitz (1896) was the first to describe an interchange of fibres between the two muscle layers, describing fibres which enter the taeniae from the circular stratum. Landau (1922, 1928) observed the passage of small fascicles of muscle between the two layers not only at the taeniae but in the intertaenial zones as well. Lineback (1925) using microdissection described large interconnexions (Fig. 6) of muscle fibres as passing from the circular into the longitudinal layer at the mid-region of the taenia by turning sharply at right angles. Austoni (1937) disagreed, in that he thought the muscular connexions to be few and of no functional significance: the important feature to him was the constant presence of a connective-elastic tissue union between the two layers. There is no doubt that the muscle layers are intimately bound together. Though no direct confirmation of Lineback's findings could be obtained at microdissection, the use of histological methods have shown that the longitudinal fibres near the borders of the taeniae change direction suddenly and, interlacing with the more peripheral longitudinal fibres, often in relationship to blood vessels, course towards and ultimately fuse with the main circular muscle layer. These fibres are found only towards the borders of the taeniae, not primarily in the middle as described by Lineback (Pace, 1966, 1968). Such an arrangement tends to retard contraction of the circular muscle layer beneath the taenia. Furthermore, though dissection shows that the connexions between the layers are not very strong, nevertheless the linkage is such as to allow the circular muscle a point of purchase for contraction and pull against the fixed taenial cables, so checking any tendency of the circular muscle to draw in at the taeniae. Both these factors tend to limit the formation of interhaustral clefts to the zones between adjacent taeniae.

AN ACCOUNT OF THE RELATIONSHIP OF THE FINDINGS TO PROBLEMS IN OTHER DISCIPLINES This is a subject that has hardly been considered for 40 years. The original impulse that led to the dissection of the colon by a radiologist was the need for an explanation of haustration and for the origin of diverticula, and in this it is a report of failure. Clearly a search for simple explanations can be a major biassing factor. It is well to remember that in many of these problems demonstrating an organizational pattern consists of exploring a preconceived idea rather than simply looking and hoping. The solutions may come easily to those investigators who possess the necessary imagination.

Prosser (1962), reviewing the work on ganglionfree circular muscle of the cat small intestine, found that contractile activity occurred in circumferential bands of about 1 mm in width, but that stimulation and electrical conductivity needed only 100 μ width of muscle. The coincidence of these measurements with those of the bands and fasciculi reported here suggests at once the need for experimentation to decide if the expanding meshwork with its mechanical suitability is also of the correct size to function in accordance with present ideas on smooth muscle contraction. The network arrangement, with fasciculi connecting the bands at intervals, should this turn out to be an organization common to gut circular muscle at all levels and in all species, might also explain the spread of contraction at right angles to the long axis of the muscle cells, which is 10 times slower than in the line of the cells and stepwise in pattern. Later work (Kobayashi, Nagai, and Prosser, 1966), discussing the electrical interaction between the longitudinal and circular layers, demands small muscular interconnexions, and this and another paper (Pace, 1968), in confirming the views of Austoni (1937), clearly records their existence in the human colon. A further difficulty arises for those who believe that infolding of the wall between two taeniae, which is seen in haustral plicae and in diverticular disease (Morson, 1963; Williams, 1963; Fleischner, Ming, and Henken, 1964), is due to contraction of circular muscle. This would require a major and persisting contraction of one or two bands over one-third of their circumference without spread of activity around the remainder and would demand some special organization or control, not absolutely impossible (Sperelakis and Prosser, 1959) but as yet undescribed.

The taeniae in their general structure and toughness resemble the suspension cable simile. What is still not clear is how they widen to accommodate the increased circumference of distension. Austoni (1937) believed that the lower mosaic portions are continuous with the intertaenial longitudinal muscle and can move sideways while still being attached to the circular layer. Nothing was observed to support this thesis, neither was the exact mechanism shown.

In diverticular disease there is argument about the presence of muscular hypertrophy, and it is obvious even from this small series that it is dangerous to attribute an increase in thickness of muscle to hypertrophy before the effect of contraction is assessed (Arfwidsson, 1964). In contraction the nuclei of muscle cells are said to be wide and short (Freeman-Narrod and Goodford, 1962) as opposed to the wide and long nuclei of hypertrophy (Arfwidsson, 1964) and this may turn out to be a decisive distinction. In a similar manner the visual prominence of Auerbach's plexus in the diverticular colon has caused difficulties in the distinction between the geometrical condensation of contraction (Morson, 1963) and hyperplasia (Celio, 1952).

Finally there are four interesting anatomical problems which look as if they should have a simple answer but none was found. What the anatomists call an interhaustral plica, which persists after death, is due to an infolding of the wall of the colon between two taeniae, though the mucosal plica on the lumen side which determines the radiographic indentation may extend around a greater proportion of the circumference. They are classically, and recently by Fleischner *et al* (1964), said to vanish when the taeniae are dissected off, and the obverse of this, that the folds can be made more prominent by contracting the longitudinal muscle and distending the circular muscle, has been shown by a mechanical trick (Williams, 1967). Many have blood vessels in

their furrows (Lineback, 1925) and they give a repeatable radiographic pattern up to 18 months apart (Halls and Young, to be published). These observations suggest that the intertaenial wall always folds in the same place, determined by the relationship of circular to longitudinal muscle. One would expect a mechanical arrangement in the muscle layers to mark the point of folding but in spite of repeated searchings by both of us, no explanation satisfactory to all areas of the colon was demonstrated. If other observers can confirm Lineback's account an explanation is at hand. With contraction of the taeniae, the circular muscle would fold at the point marked d in Fig. 6, somewhere between the points at which his taenial fascicles turn at right angles into the circular layer.

Some authors, and among the recent ones are Painter and Truelove (1964), subscribe to the idea of segmental activity in the colon. No anatomical basis for such segmentation could be recognized in the muscular layers.

In view of the still unresolved argument over the emergence of diverticular sacs in relationship to blood vessels (Fleischner *et al*, 1964; Slack, 1960) an unrewarded attempt was made involving the dissection of some 50 sacs to find an explanation in the arrangement of the muscular wall. Note that Lineback's taenial fascicles (Fig. 6) are drawn as turning into the circular muscle and terminating at the point on the circumference at which many sacs emerge (Slack, 1960). If his account could be confirmed, contraction of the taenia might result in the partial withdrawal of these fascicles from the circular layer leaving a gap through which mucosa could herniate.

It would be helpful to elucidate the methods whereby the taenia and circular muscle change shape from contraction to distension. When the lumen diameter increases twofold, does each cell in the circular layer elongate to twice its length or is there an arrangement whereby cells or groups of cells can slide over each other increasing the length and reducing the depth of a fasciculus? A sliding mechanism has been argued for heart muscle (Linzbach, 1960) and suspected for smooth muscle (Gillespie, 1962). Change in the shape of bands and fasciculi (Fig. 8a) is in favour of sliding groups of cells, and the rapid change in depth of the fasciculi at haustral folds seems to need some mechanism additional to a change in cell length. Indeed, by the time this work was finished, a strong suspicion had developed that much of the apparent solidity of the fasciculi was the result of formalin fixation and that they must have in life a more fluid arrangement. Histologically small separated groups of cells were seen, but not with enough regularity to give an acceptable account of a sliding mechanism. A limitation of the capacity to slide could be part of the perpetuating mechanism of a myostatic contracture (Williams, 1965).

SUMMARY

A coordinated account is presented of two independent investigations of the muscular layer of the human colon, a subject poorly studied in the past. The conclusions represent the subjective recognition of organizational patterns in formol-saline-fixed operative and postmortem specimens, mainly from the middle-aged and elderly, and assessed predominantly by dissecting microscope techniques.

The circular muscle is an expanding meshwork of interlinked bands of the order of 1 mm in width. Each band is divisible into fasciculi of the order of width of 50 to 200 μ .

Longitudinal muscle is continuous over the whole colon, in the intertaenial areas as a thin banded structure. The taeniae have a banded structure in the outer half but in the deeper layers are in groups of cells separated off giving a mosaic appearance in transverse section. This level contains much connective tissue and the taeniae are more closely woven solid structures than circular muscle.

The circular muscle is firmly attached to the underside of the taeniae, more so at its edges, by connective tissue and muscle cell groups, the latter of a size only clearly recognizable by histological techniques. The two of us differ on the certainty and importance of these linkages.

A brief study of distended and collapsed colons showed a number of features relevant to the pathological concepts of hypertrophy and hyperplasia.

A successful relating of these findings to recent physiological ideas of smooth muscle contraction would help in the interpretation of radiographs. No explanation in the muscle layer could be found for the anatomy of haustration, the origin of diverticular sacs, or the sequential nature of colon contractions.

ADDENDUM

Elsen and Arey (1966), using dissection of fresh specimens to determine whether the gut muscle has a spiral organization, present results which partly confirm and do not conflict with the findings of the present paper. Some additional reference to the problem of the muscular structure of intestine in general will be found in their paper.

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