Colonic motor activity and bowel function

Part I  Normal movement of contents

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There have been few detailed accounts of human colonic movements since the original radiological observations on animals by Cannon (1901).

Holzknecht (1909) described as a 'mass peristalsis' a wave of contraction that moved down a narrowed section of colon from which the interhastral folds had temporarily disappeared. The remains of a bismuth meal were propelled in this way in seconds from the transverse colon to the pelvic colon, leaving the gut empty behind it. Holzknecht saw no other changes in the outline of the gut wall and concluded that the activity of the normal colon was limited to such sudden, brief and occasional movements, occurring perhaps three times in a day.

Schwarz (1911) made repeated tracings of the outline of the colon on a fluoroscopic screen after a bismuth meal and showed that its haustration was slowly changing for much of the time. Haustral movements were most common in the proximal half of the colon, and travelled a little way backwards and forwards along the bowel.

Hertz and Newton (1913) described small rapid movements in the haustra of the caecum and ascending colon. In addition, they observed a propulsive movement which, though it also involved ingested bismuth and was associated with a transient tubular appearance of the colon, was otherwise different from that of Holzknecht. It occurred when some of the contents of a distended section near the hepatic flexure were transported almost instantaneously to the splenic flexure without emptying the original section. Hertz and Newton considered that such a movement of the contents could only have been effected by a uniform circular contraction of the distended section of colonic wall. Hertz (1909) had already noted that colonic contents observed over long periods appeared to travel farther during the dinner hour than during any other four-hour period.

Barclay (1912) also observed mass movements in the human colon, and later (1935) was able to demonstrate haustral movements in the transverse and descending colon by x-ray cinematography during periods of up to two and a half minutes. He described the movement of hastral contents as being slow, intermittent and circular within the hastrum, with no sign of directional intention. Ritchie, Ardran, and Trueove (1962) observed the secondary contraction of individual haustra in the pelvic colon some four to eight seconds after their distension by injected liquid, and distinguished what appeared to be longitudinal and circular components of such contractions. Serial contraction of liquid- and gas-filled haustra produced a segmental propulsive movement away from the site of introduction of the liquid at widely varying speeds up to 4 in./sec.

The mass propulsions originally described by Holzknecht and by Hertz and Newton seem to have since come to be regarded as identical and, by some observers, as synonymous with peristalsis. However, peristalsis is not usually associated with the tubular appearance that precedes mass activity. The classical description of Bayliss and Starling (1900) makes it clear that they regarded peristalsis as essentially a progressive wave of contraction preceded by a wave of relaxation. Peristalsis within this strict definition, though called a 'stripping wave', has recently been described in detail by Williams (1967) as a feature of the evacuation of barium enemata to which 2% of Dulcolax had been added. These 'actuated' waves propelled liquid bowel contents at varying speeds between the slowest visible advance and about 3 in. (8 cm)/sec, and the relaxation ahead of them was sufficient to relieve the spastic structures associated with diverticulitis. Barclay (1936) expressed the opinion that propulsion at a greater speed than this was likely to be abnormal. The only peristaltic movement observed by Ritchie et al (1962), which was probably transporting semisolid bowel contents, travelled at a maximum speed equivalent to less than 6 in. (15 cm)/min.

In view of the scarce and sometimes contradictory nature of these observations, a study was made of
the radiological appearances of ingested barium in the human colon. It was undertaken in the first place to examine the character and to establish the frequency of the movements of normal contents in the bowel. In Part II of this study, the distribution of the different movements within the colon and their relationship to its function will be examined in more detail.

TECHNIQUE AND APPARATUS

Each of the 193 subjects examined had been given barium sulphate suspension by mouth and between 12 and 24 hours later the colon was observed in the supine position to avoid compressing the bowel. The barium was first located briefly by means of television fluoroscopy and the subject was positioned to ensure that maximum advantage was taken of the whole field of the 12½-inch Cinelux electron-optical image intensifier. No other monitoring was attempted; experiment showed that on average five seconds of fluoroscopy represented the same exposure to radiation as 13 frames of cinefluorography.

The 35 mm time-lapse cinefluorography was maintained for one hour at a rate of one frame per minute. In this way the almost imperceptible movements of the normal colon could be accelerated several hundred times. Details of the rapid movements involving gas or liquids, as seen in barium enema examinations, tended to become unrecognizable. However, the transport of gas was outside the scope of this study and even fresh ileal contents on entry to the colon were rarely seen to cause such rapid changes of outline.

Each colon was observed without any subject receiving more than 775 R cm$^2$ to an area of about 450 cm$^2$. Over the whole series, the mean irradiation was less than half this figure, 295 R cm$^2$, a skin exposure of about 0.75 R.

CLINICAL MATERIAL

The subjects included in the present study were convalescent volunteers from among the ward patients of the Radcliffe Infirmary, Oxford. They offered to help after the purpose of the work and the possible dangers of the small amount of radiation involved had been fully explained to them. Their ages ranged from 22 to 87 years although, as a general rule, women of childbearing age were excluded. Nineteen (10%) of the subjects were known to have colonic disease. One hundred and one of the subjects were observed for the whole hour under resting conditions, 63 were given their ordinary ward lunch to eat at the start of the period of observation, and 29 were given an intramuscular injection of 0.25 mg of carbachol instead. The interval before the earliest recognizable gastrointestinal response to carbachol, which was usually an increase in ileal outflow, varied from three minutes to more than 40 minutes (mean 11 minutes). In about 10% no ileal response was visible. Any increase of colonic propulsion that occurred usually began later, between 15 and 45 minutes after the injection.

Both food and carbachol were found to alter the incidence, and probably the speed, of colonic activity but there was no evidence that they changed its character in any way. Some of the more extensive movements of colonic contents were relatively uncommon under resting conditions and, because of superimposition by barium in other sections of gut, were often unsuitable for reproduction as illustrations. When necessary, the corresponding movements seen in stimulated patients have been used instead. The illustrations were all taken from different subjects.

INTERPRETATION

The displacement of normal colonic contents is unlikely to have any other propulsive source than the contractions of the bowel wall surrounding them. However, it must be borne in mind that it is only the barium-impregnated contents themselves that can be seen with certainty in these fluorographic studies, and that gut movements which are envisaged to explain changes in their outline can only be deduced.

RESULTS

The normal appearance of the mass of colonic contents at rest varied widely between those that were relatively narrow and almost ribbon-like, and others that were broad and had a deeply indented outline. In some colons the haustral barium masses were unconnected by contrast medium. Occasionally a section of six or eight inches of segmented bowel contents might become smooth-edged one minute and then revert to its former haustral pattern, or to a different one, in the next.

NON-PROPULSIVE SEGMENTAL MOVEMENTS The cinefluorograms showed that over the period of observation there was almost always movement of some kind somewhere in the colon. Only in one subject did the whole bowel appear to remain immobile throughout the hour, and even then there may have been some movement of gas in the intervals between radiographs.

The commonest movement of colonic contents consisted of a change in the outline of the barium mass where some degree of continuity existed between adjoining segments. These changes were of great variety. The simplest took the form of a reduction in the dimensions of the haustral barium mass, chiefly affecting its diameter at right angles to the long axis of the gut, with displacement of a proportion of its barium into neighbouring haustra. Such a change sometimes reduced the volume of the mass even to complete obliteration in from less than a minute to about five minutes, and lasted for less than a minute or up to half an hour. The escaping barium travelled in both directions equally, or predominantly forwards or backwards, and after an interval of similarly
variable duration it either returned to its previous site or moved still farther in the same direction.

The constriction between two haustra varied in depth from nothing to one producing complete isolation of the contents. Its width varied from less than a tenth of an inch up to two inches or more, occasionally changing from one to the other in the course of a few minutes. This change sometimes extended symmetrically up and down the bowel or in one direction only, moving steadily forward as the barium mass ahead of it was shortened and displaced, or advancing abruptly with the emptying of a whole haustrum at a time. Sometimes a constriction, without varying its width, progressed an inch or so in either direction along the bowel allowing the barium ahead to escape back through it.

The indentations in the surface of the barium mass often matched one another on the two sides of the gut, but sometimes those on one side were offset slightly and appeared to alternate with those opposite them. Occasionally fresh constrictions appeared in the outline of a barium mass, adding temporarily to the total number present in that section of bowel. Usually this was followed within the hour by the disappearance either of the newly created indentation, or of another one nearby, to restore the relations of what appeared to be an optimum haustral pattern for the individual under the conditions prevailing at the time.

In 38% of the subjects observed at rest this random haustral shuttling without recognizable propulsion was the only form of movement seen (Fig. 1), but the proportion fell to about 13% after food or carbachol injection. Whole sections of an individual subject’s bowel might remain apparently immobile throughout the hour whilst movements continued to occur elsewhere. The local incidence of movements of this kind will be described in detail and discussed in the second part of this study. Sectional immobility was particularly noticeable in the rectum, where no change in outline could be seen in 60% of the observations made at rest or after food.

In the transverse colon, on the other hand, there was haustral activity somewhere during some part of the hour in all but 10% of subjects.

**PROPULSIVE MOVEMENTS** Amongst the remaining 62% of subjects, at some time during the hour of observation, segmental activity developed locally into a true propulsive or retropulsive movement; contents travelled through two or more adjoining haustra and their return, for a time at least, was blocked. The movements concerned in the transportation of barium either involved the systolic contraction of haustral units, singly or in groups, or they resulted from a continuous wave-like progression of interhaustral activity.

When the contents of individual haustra were

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**FIG. 1.** Proportion of subjects showing colonic movements at rest and after food and carbachol.
Colonic motor activity and bowel function

In the following illustrations the prints have been taken from cine-fluorograms, the time intervals between them being indicated in minutes.

FIG. 2. Segmental propulsion and the development of coordination.

Successive haustra in the transverse colon of a subject with normal bowel function have been lettered for identification. Increased ileal outflow in the 15 minutes after an injection of carbachol had distended the ascending and proximal transverse colon as far as haustrum a in the first print. After one minute, contraction of part of the transverse colon, including haustrum a, transferred additional barium to haustra b, c, and d. When c and d contracted a minute later, a small proportion of their barium moved adorally to b and the rest aborally to e, f, and g. In the same way, when f contracted two more minutes later, its contents were shared between e, g, and h. After another minute, g also contracted and most of its contents went on to distend h.

Over the next eight minutes, contractile activity took place in a different form. In the sixth and seventh prints, taken at two-minute intervals, the haustra e, f, and g shortened adorally and widened, and the successive elimination of their interhastral divisions incorporated first f and then g into a single unit with haustrum e. When, over the next four minutes, the e-f-g group unit returned to its original dimensions, and its haustral pattern began to be restored, barium from e had effectively been transferred to f and g.

displaced aborally one at a time, either serially or sporadically, the movement is referred to as haustral propulsion. If a number of haustra were simultaneously involved in activity as a coordinated unit with their contents pooled, the propulsion is said to be 'multihaustral'. When the barium mass became narrow and ribbon-like ahead of multihaustral activity and contents travelled eight inches or more in a single movement, this is described as 'mass' propulsion.
Haustral propulsion The simplest propulsive movement of all occurred when the contents of a single haustrum were displaced by systolic contraction into the next distal segment, and thence on to one beyond it instead of being returned to the first.

Haustral propulsion of this kind is illustrated in the first five pictures of Fig. 2, which show contents from the proximal colon travelling aborally through successive haustra. Contraction of the dimensions of a distended section of the proximal transverse colon, which includes the haustrum lettered a, displaces a proportion of its barium contents into an adjoining section, comprising haustra b, c, and d. Subsequent contraction of individual haustra there, in particular c and d, expels the barium in both directions, but chiefly in the direction of the original thrust to e, f, and g. Two minutes later, the propulsive process is repeated farther along the bowel; the contents of haustrum f are displaced distally to distend h, and after another minute the contents of haustrum g move to join them. In this instance, propulsive activity involved a section of bowel about 7 in. long between haustrum a and haustrum h, over a period of five minutes.

In the last five pictures of Fig. 2 haustral propulsion of a different kind is visible in the three haustra lettered e, f, and g, which show progressive shortening and broadening of their outline. At the same time the space between g and h is becoming longer and narrower, and the interhaustral folds between e, f, and g disappear. After about four minutes the three haustra are seen to have merged into one. A minute later, the three haustra have recovered their original length and their circumference is reduced once more. In the final picture of the series, when the first interhaustral fold is restored between e and f, most of the original contents of haustrum e have in effect been transferred to f and g.

Whether the shortening of the three haustra, e, f, and g, was due to longitudinal contraction or not is impossible to say with certainty. However, in the lower row of pictures in Fig. 3 there is definite adoral movement of a diverticulum attached to the
gut wall as a broad column of barium contents is forced towards it. The upper row of pictures illustrates an earlier advance by a narrow ribbon of barium, which caused no such longitudinal response.

Haustral propulsion took place in some part of the colon during the hour of observation in 36% of subjects under resting conditions, many of them showing two or more separate propulsive movements over the period. After lunch its incidence increased to 57% of subjects and after 0.25 mg of carbachol 52% showed this form of propulsion (Fig. 1). Haustral propulsion might travel any distance from about 2 in. up to 8 in. and possibly farther (mean: 2.75 in.) at approximately 1 in./min. However, over the whole length of the colon, the net propulsive effect was less than might have been expected. Haustral retropulsion, an identical but adoral displacement of gut contents through two or more haustra, was about two-thirds as common under resting conditions as haustral propulsion, both for short-distance (< 3 in.) and long-distance movements.

Haustral retropulsion occurred in 30% of colons during the hour and in more than half the instances in which it was observed there was also some form of propulsion during the actual period of study. After lunch, retropulsion was present in 52% of the subjects and most of these showed propulsion at some point as well. Carbachol injection was followed by retropulsion in only 38% of subjects, and this is not significantly more in statistical terms than the incidence at rest. Incidentally, in almost all the 87% of subjects who showed any displacement of contents in either direction during the hour after carbachol, it caused more than one form of movement.

**Multihaustral propulsion**

Multihaustral pro-
pulsion showed the same general pattern of contractile activity as hastral propulsion, but it affected three or more segments together as a coordinated unit, with their interhastral folds partly or wholly obliterated. There were two forms, which are described as 'systolic' and 'serial'.

Systolic multihaustral propulsion, about four times the commoner of the two, was seen when a number of segments in the proximal colon appeared to contract more or less simultaneously. Part or all of their contents went distally to distend an adjacent length of bowel and the interhastral folds in the recipient section were usually effaced at the same time.

A train of three systolic multihaustral contractions in succession over a period of less than 10 minutes is seen in Figure 4. In the first print, barium was passing through the ileocaecal valve to distend the entire right colon. When the right colon contracted three minutes later, several haustra at the hepatic flexure were able to accommodate its surplus contents for two minutes before they themselves contracted. Their barium went on to fill seven or more haustra in the proximal transverse colon, and again the interhastral constrictions disappeared in response to the distension. After another four minutes this section also contracted as a whole and the displaced barium advanced towards the splenic flexure. The mean rate of propulsion over the whole train of movements was about 2 in./min.

Serial multihaustral propulsion originated in the same way, with the displacement of barium from a number of haustra in the ascending or proximal transverse colon. The barium distended a short length of bowel farther distally, usually comprising four or five haustra, from which the hastral pattern disappeared. At this point the movement was indistinguishable from that seen in the previous figure. Then, instead of the group of recipient haustra contracting together to produce another systolic type of propulsive movement, the proximal segment only of the multihaustral unit appeared to recover its original size and haustration (Fig. 5). Its surplus contents joined those already filling the...
other three haustra that made up the tubular section. After a short interval, the outline of the next haustrum beyond the distal end of the section also became distended and was incorporated into the multihaustral unit. The process was repeated at intervals, usually of between about 30 seconds and three minutes, and in this way the tubular section with its extra barium contents moved along the gut, one haustrum at a time, at about 1 in./min.

Multihaustral propulsion of one kind or the other was present at some time during the hour in 9% of subjects at rest. After food it occurred nearly twice as often (Fig. 1), but this difference over the whole study is not statistically significant. After carbachol injection, which was a much more powerful stimulus, it was seen in 41% of observations.

Similarly coordinated retropulsive movements were not seen in any subject with a normal bowel, but three occurred in patients with colonic pathology. Figure 6 shows a succession of systolic multihaustral retropulsive movements occurring at rest in a patient with mild ulcerative colitis and moderate diarrhoea. The distribution of barium shows that there is a closed and empty sigmoid colon and rectum, and a more open and poorly segmented descending colon.

INTERHAUSTRAL PROGRESSION Progressive activity took the form of annular constrictions of the barium mass, which appeared to originate as interhaustral folds and advanced more or less steadily along the bowel in either direction like waves.

This sort of progression, with or without propulsion of the barium held between the constrictions, is most readily demonstrated in patients with uncomplicated diverticulosis of the colon. In Fig. 7, three interhaustral indentations in succession, those between the haustra a and b, b and c, and c and d, appear to move aborally past a small stationary diverticulum (arrowed 1) in the distal transverse
FIG. 7. Progressive movement in the transverse colon.

At the time of the first print in this series, which begins 15 minutes after an injection of carbachol, barium from the terminal ileum was entering the proximal colon. Two small asymptomatic diverticula from the transverse colon, marked 1 and 2, showed by their position in relation to the interhaustral constrictions in the barium there the movements made by the gut wall. The relevant haustral barium masses have been lettered.

The more distant of the two diverticula (I) was attached originally to the gut wall marking the proximal aspect of the barium mass labelled a. Over the duration of the series of pictures, the barium masses marked b and c and their intervening constrictions were seen to travel aborally past it.

During the first five minutes of the period of observation, the haustral barium masses in the proximal transverse colon moved aborally together. The second diverticulum, which was attached to haustrum g, moved towards the hepatic flexure with the haustrum. Their relationship was maintained for at least the next 15 minutes, showing that the movement in this instance could not have been progressive.

Although the presence of diverticula in the transverse colon on this occasion facilitates the demonstration of progressive activity, in the descending and sigmoid colon diverticular disease may sometimes interfere with peristaltic movements.

A relatively large proportion of these contraction waves were seen to travel the length of one haustrum or even less; others were too shallow to stop gut contents escaping back past them, and these both formed part of the haustral mixing mechanism. Waves that advanced through two haustra or more were potentially propulsive, and provided the foundation of peristalsis.

Peristalsis In Fig. 8 an interhaustral constriction appeared in the distended ascending colon five minutes after an injection of carbachol. It extended aborally with a steady progression, carrying the barium mass distal to it round the hepatic flexure...
and through the transverse colon for six or eight inches, at a mean speed of about 0.5 to 0.7 in./min. The mass was preceded by gaseous distension of the bowel and followed by an increasing length of closed and empty bowel. This remained contracted for about seven minutes, but when gas returned to it, it refilled evenly over its whole length. Shortly afterwards, there was a second peristaltic movement over much the same course, which has not been illustrated, but which advanced at about the same speed.

Peristaltic movements thus appeared to combine over several colon segments three forms of activity in varying degrees and proportions. These were the progressive wave, as demonstrated in Fig. 7, with muscular relaxation preceding it which was frequently outlined by gaseous distension, and with tonic muscular contraction reinforcing it from behind. This tonic contraction, apparently both circular and longitudinal, kept the bowel closed and empty afterwards for periods of from five minutes to an hour or more.

Peristalsis was seen in 6% of colons at rest during the hour, most commonly distal to the midtransverse colon. The proportion rose only to 8% after lunch. Carbachol stimulated a much greater increase and, after the injection, peristalsis was present in 28% of subjects. Peristalsis could also be reversed, though this was relatively rare; it was only seen on one occasion in this series, in a normal subject after carbachol. Reflux peristalsis is much commoner in the irritable colon syndrome.

**MASS PROPULSION** Mass activity tended to start about the middle of the transverse colon and appeared to need some form of generalized contraction in the right colon to 'prime' it. Usually this took the form of a multihaustral propulsion. The mass propulsion
FIG. 9. Mass peristalsis (illustration borrowed from another study).

At an earlier stage in the examination of this patient with spastic colon and pain in the left iliac fossa, barium had been introduced through a tube into the sigmoid colon. In spite of much subsequent activity there, none of it passed adorally through the painful section at P, and discomfort was felt there at each retropulsive movement. Carbachol had been given about half an hour before the start of this series of cinefluorograms.

Five minutes before the first print, two barium scybala, a and b, had traversed the empty transverse colon to the splenic flexure and passed out of the field of the image intensifier. Three others (arrowed c) remained in the transverse colon at the time of the first picture. Over the next four minutes liquid barium from the right colon was transported, probably by serial multihaustral propulsion, through the transverse colon past the group of scybala at c, which were themselves held fast in position, apparently by their interhaustral folds. After another minute, in the fifth frame, the scybala at c were seen to move briefly towards the hepatic flexure. The peristaltic movement that followed two minutes later carried the scybala with it and developed rapidly into a mass peristalsis with the characteristically narrow and ribbon-like barium column in the descending colon. However, the progression of interhaustral constrictions surrounding the two leading scybala, which appeared to be a and b from the splenic flexure, kept them separate both from each other and from the liquid contents behind them.

might develop directly from it, or a peristaltic movement might intervene, especially when there were solids to be transported along with other contents. The two forms each occurred on four occasions most commonly after food or carbachol. In both of them, the configuration of the barium
ahead of the propulsive movement indicated that it was advancing into a narrow, tubular section of bowel, which was at least 8 in. long.

An example of mass peristalsis is shown in Fig. 9, which has been borrowed from another study because it shows most clearly the development of this form of propulsion. The subject had spastic colon with pain in the left iliac fossa centred over the distal descending colon near P in the first picture; she had previously had pressure-recording tubes introduced at sigmoidoscopy and she had been given an injection of carbachol 25 minutes earlier. At the time the first picture was taken there appeared to be hard scybala in the mid-transverse colon (arrowed c) and two others, a and b, had recently passed through to the splenic flexure, outside the field of the image intensifier. The first four pictures show fresh ileal contents from the ascending colon being propelled past the solids in the transverse colon, probably by serial multiaxial activity, without displacing them. After that the scybala themselves become involved in a peristaltic movement and are propelled towards the splenic flexure. Over the next five minutes mass peristalsis develops in the transverse and descending colon and the barium advances rapidly to about the site of the patient's pain. Two scybala, which are probably a and b from the splenic flexure, are moved ahead of the more liquid contents instead of being submerged by them and are kept separate also from one another by their advancing interhastral constrictions. The remainder of the barium in the descending colon is typically ribbon-like. The mass propulsion came to an end in this instance because the peristaltic wave itself stopped when it reached the painful zone of the spastic colon; the mechanism of propulsion in that section appeared to be abnormal.

Mass propulsion transported the bowel contents at varying speeds, often as far as the pelvic colon. Their rate of propulsion could not always be measured with accuracy, partly because it altered from minute to minute, but chiefly because of the difficulty of identifying specific contents to decide how far they moved. When barium travelled in this way through an empty length of colon it was most commonly at about 1 in./min over 2 ft or so of bowel. However, in one instance the rate was nearer 2 in./min and in another the mass of barium advanced a distance of about 12 in. in four minutes. Once, again, barium crossed the transverse colon, a distance of at least 12 in., at more than six in./min after an injection of carbachol.

The lack of a sufficient degree of narrowing or of tubularity in the gut ahead of the movement at the outset of activity seemed in a number of instances as though it could abort the development of mass propulsion. In the same way, either persistence of haustration distally, or local relaxation and distension of the tubular section of bowel as seen at d in Fig. 3, was enough to arrest its progress. Retropulsive analogues of mass propulsion were not observed.

The propulsive complex of movements by which evacuation is sometimes achieved, and for which the term 'mass movement' has been reserved, was not seen in actual operation in the present study. Figure 10 was taken from a subject with normal bowel function who asked to be allowed to defaecate during the period of observation. It shows the effect of a systolic type of multiaxial contraction involving the distended rectum and distal sigmoid colon. This initiated a retropulsion into the pelvic colon, whilst at the same time the reactive thrust of the rectal contraction against the anal sphincter was evidently strong enough to provoke an urgent call to stool. The mass movement that followed emptied almost the whole distal half of the colon, apparently by mass peristalsis.

It is of interest to note that only about one third of the subjects whose bowels had acted before the study showed evidence of having experienced a mass movement on anything approaching this scale. The other two-thirds appeared to have had a systolic type of contraction involving the rectosigmoid region only and leaving the rest of the distal colon unaffected. A number of them reported the action as having been difficult or otherwise unsatisfactory, but many were content and clearly regarded this procedure as normal.

**DISCUSSION**

The transport of normal colonic contents took place at speeds which were 30 to 100 times slower than those at which gas and artificially introduced liquids have been seen to travel (Ritchie et al., 1962). Often the movements took several minutes to complete. Such propulsion is different from that seen in the course of barium enemata, and can only be observed and analysed by means of time-lapse cinefluorography.

Non-propulsive segmental activity results in short-range movements of the colonic contents, through localized contractions of the gut wall; as Connell (1962) pointed out, it is essentially obstructive in operation. The movements must be regarded as homogenizing the contents and increasing both the pressure of their contact with the mucosal surface and the area over which this takes place; in this respect, they appear to be chiefly concerned with the absorption of water and salts (Anderson, Schmidtke, and Diffenbaugh, 1962). As Schwarz
(1911) noted, this form of activity was commonest in the proximal half of the colon. Levitan, Fordtran, Burrows, and Ingelfinger (1962) found absorption to be most efficient in this part of the bowel.

Haustral propulsion has all the characteristics of non-propulsive segmental activity with an aboral gradient of movement: Bloom, LoPresti, and Farrar (1963), using radiotelemetering equipment, claimed a difference of basal pressures between the right and left sides of the normal colon amounting to about 26 cm of water. The 67 hastral propulsive movements seen in the present study advanced the colonic contents by an average distance of almost 3 in.; during the same period 44 comparable retropropulsive movements returned contents over an average distance of two and a half inches. This activity increases mean pressures and probably assists absorption. Only about half of all hastral propulsion at rest is effectively propulsive.

The reinforcement of hastral activity by longitudinal or progressive contractions, which took place on several occasions, especially in the transverse colon, gave rise to the simplest form of coordinated propulsion. It may never be possible to record intraluminal pressures simultaneously from a number of consecutive haustra in the transverse colon with synchronized cinefluoroscopy, so it may be worthwhile to speculate upon the mechanisms apparently involved. In Fig. 2, for example, the original distension and subsequent contraction of the ascending and proximal transverse colon seems to have established an aboral gradient of pressure in its contents, which was still in process of equilibration seven minutes later. This, and the partial closure of the interhaustral fold between d and e, would have helped to ensure that a contraction of the dilated haustrum e should expel its contents distally. On the other hand, as anyone who has blown up a long balloon will know, it is much easier to inflate a section with a large diameter than one that is narrower; the small diameter of the haustra f and g would have made them difficult to distend with contents from the larger haustrum e unless the muscle tone of their walls was lowered. Since haustrum g was still contracting, the muscle tone or resistance to distension in its wall was almost certainly higher than that at e, and this would have hindered any further advance of contents from haustrum e. By drawing the three haustra together, and first pooling and then redistributing their contents, much of the muscular effort that would have been needed to fill f and g by a circular contraction of e against resistance was avoided.

The mechanism whereby several inches of bowel, unable to produce a systolic type of propulsive contraction against resistance, could still manage to advance their contents by longitudinal shortening is not clear. In Fig. 3 the appearances did not indicate a simple taenial contraction, as the interhaustral folds were not telescoped. Probably the shortening was produced by the oblique component of the lattice-work of circular muscle fibres, when the circular component of their contraction was obstructed. In extreme cases, longitudinal contraction
seemed in effect to draw the gut wall lengthwise over the solid masses inside it.

**Propulsion in the proximal colon** Systolic multihaustral propulsion usually began with a generalized contraction of the right colon some time after that section had been distended with fresh ileal effluent. There was thus inevitably a substantial gradient of intraluminal pressures between the blind end of the caecum and the transverse colon. Under these conditions the bowel contents, which were semiliquid and more or less homogeneous, were only able to escape in one direction.

Serial multihaustral propulsion, which began apparently in the same way, was most commonly seen when fresh ileal effluent was transported over the surface of more solid contents. It was not seen to pass beyond the splenic flexure. Because haustration was maintained ahead of the advancing liquid and the folds were restored immediately behind it, the bowel was able to hold back individual scybalae, as in the first half of Figure 9. This form of propulsion provides a means of softening hard contents to make their future movement easier.

Mass activity provided the most effective means of extending multihaustral propulsion into the distal colon. Its chief point of distinction was the narrow, tubular appearance of the gut wall ahead of the original multihaustral contraction. As described by Hurst (1919), mass propulsion occurred most commonly after eating, and six out of eight instances in the present study were associated with either food or carbachol. Eating can be shown to stimulate the ileal outflow, and to narrow the gut and increase its resistance to distension, and carbachol injections have the same effect. Under normal conditions the hypertonus of mass propulsion may represent, in part at least, the effects of the various feeding reflexes. For a given pressure gradient, the speed and extent of the propulsion is determined by the diameter and tone of the bowel, and by the consistency of its contents. The most rapid and effective movements were those that occurred after carbachol; even so, in normal subjects, the maximum rate of propulsion was only about one-tenth of an inch per second.

**Propulsion in the distal colon** Contents distal to the mid-transverse colon have often been reduced by absorption to a firmer consistency, and their transport and elimination seemed to require a different form of motor activity. Any method of propulsion that uses circular contraction to move a solid mass lengthwise by uniformly reducing its circumference, however steep the pressure gradient, is extravagant of muscular exertion. Moreover, because reduction of the gut diameter beyond a certain degree increases its resistance to the passage of solid contents, the propulsive power of a systolic contraction can only be increased to a limited extent by strengthening the contrac tile effort.

Peristalsis appeared to offer a more efficient and economical form of propulsion. The muscular effort involved in contracting an interhaustral fold one-tenth of an inch or so in width to divide up a solid mass of gut contents is relatively small compared with that required for a comparable uniform circular contraction over, say, a 3-in. length of bowel. The "push-pull" displacement of the scybalum so formed into a relaxed section of colon ahead of it can add little to the energy requirement; it involves a combination of wave progression and longitudinal contraction, acting proximal to the mass and so in effect drawing the gut up over it, as originally described by Bayliss and Starling (1900).

The mechanism of peristalsis, unlike that of segmental propulsion, appeared to be widely variable, with different proportions of coordinated muscular contraction behind and relaxation ahead of the progression. The relaxation of the bowel wall immediately ahead of a peristaltic movement could only be inferred when the contents were solid, from the outline of the gas that was often accommodated there. Under these circumstances, the presence of gas provided a major practical point of identification between peristalsis and a sequence of haustral propulsive movements, when the timing of cine exposures otherwise obscured the distinction. Relaxation was not recognizable when the bowel contents were liquid, and were transported by the same mechanism and at the same speed as the gas itself, but then it was not so necessary and may in fact have been absent altogether.

Peristalsis could even become incorporated into a mass propulsion, as in Fig. 9, to form a mass peristalsis like that described by Holzknecht (1909), though the usual rate of advance appeared to be very much slower.

**Retropulsion** Retropulsion probably resulted from a reversal of the usual aboral pressure gradients of the colon. It served to slow the overall aboral drift of contents away from the ileocaecal valve and so to provide more time for water absorption.

Another function of retropulsion in the distal bowel may be to relieve the normal rectum of contents that might be voided unintentionally with any sudden rise of intraabdominal pressure. Rectal contents which are normal in consistency and under no great pressure may readily be returned to the descending colon; Halls (1964) demonstrated it using ingested barium-impregnated polythene discs as markers. In the present study, segmental retro-
pulsion was most commonly seen in the distal bowel in subjects with a tendency to frequent bowel actions, especially when there was a tense and empty rectum and sigmoid colon (Fig. 6). Steep adoral gradients of pressure in the descending colon associated with obstruction of the distal bowel, by providing conditions comparable with those at the blind end of the caecum, might even possible lead to a mass retro-pulsion. Hertz (1908) described something of the kind occurring in a patient with carcinoma of the colon. This has not been seen in the present study, and it is unlikely to play any part in normal colonic function.

SUMMARY

Time-lapse cinefluorography at one-minute intervals over a period of an hour was used to study the character and incidence of colonic motility in 193 human volunteers at rest and after food, and after injection of carbachol.

 Movements of barium sulphate suspension ingested 12 to 24 hours earlier were divided into propulsive and non-propulsive categories. Non-propulsive segmental movements were the only form of motor activity seen in 38% of subjects at rest; propulsive movements were seen at some time during the hour of study in 62% of subjects at rest, and in 87% after food and carbachol. Normal colonic contents were transported in either direction between 30 and 100 times more slowly than liquids and gas.

 The different forms of propulsive and retropropulsive activity inferred from the movement of barium contents have been described and classified, together with their incidence at rest and after stimulation. Their relative importance and effectiveness in different sections of the bowel are discussed.

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