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COLONIC MOTILITY AND TRANSIT OF DIGESTA DURING HARD AND SOFT FAECES FORMATION IN RABBITS

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SUMMARY

1. Rabbits produce hard and soft faeces in a circadian rhythm. This study was undertaken in order to examine the motor function of the colon in relation to the formation of these two types of faeces.

2. Colonic motility was measured in unanaesthetized rabbits using strain-gauge transducers and simultaneous radiography.

3. Three types of contractions were found in the rabbit proximal colon: haustral activity, segmental activity, and mass peristalsis. Distinctly different motor patterns were observed during the formation of hard and soft faeces.

4. When hard faeces were produced, the motor activity of the proximal colon was enhanced. It consisted of segmental and haustral activity. The segmental contractions separated the digesta into faecal pellets and forced them slowly aborad, whereas the movements of the haustra carried the liquid contents back towards the caecum.

5. When soft faeces were produced haustral and segmental activity was reduced and transfer of the digesta through the proximal colon was accelerated by mass movements.

6. In contrast to the proximal colon, the motility of the distal colon was enhanced during the formation of soft faeces and decreased during the production of hard faeces.

7. The results support the concept that hard faeces are chiefly produced by a separation of liquids and solids and by a retrograde transfer of liquid digesta rather than by an increased absorption of water.

INTRODUCTION

Rabbits and some other animals eliminate, in a circadian rhythm, soft and hard faeces which are distinctly different in size and in chemical composition (Hörnicke & Björnhag, 1980). The familiar, dry, hard faeces are high in fibre and low in protein, micro-organisms, water-soluble substances, and vitamins, whereas the composition of the soft faeces which are re-ingested is similar to that of the caecal contents.

Several investigators have assumed that the alteration in composition of the hard faeces is produced by an efficient absorption of water-soluble substances along the colon, due to the slower passage of digesta (Eden, 1940; Yoshihara & Kandatsu, 1960; Bonnafous & Raynaud, 1967, 1970). Subsequent studies have shown that the formation of dry, hard faeces is not only produced by absorptive processes but also

by mechanical separation of liquids and solids during the transit of digesta through the proximal colon (Pickard & Stevens, 1972; Björnhag, 1972, 1981*a*). It has been observed fluoroscopically that contrast medium administered into the rabbit colon was swept back into the caecum by antiperistaltic waves (Pickard & Stevens, 1972; Björnhag, 1981*b*). However, the motor activity of the rabbit proximal colon in relation to the passage of digesta is poorly understood and remains to be elucidated. In previous experiments (Clauss, Ehrlein & Hörnicke, 1978) we have found, in agreement with other authors (Fioramonti, Bueno & Ruckebusch, 1980), that the motility of the proximal colon is increased during the formation of hard faeces and decreased during the production of soft faeces. The physiological significance of these findings is not known. In the proximal colon of rabbits three types of contractions can be differentiated: (1) high-frequency, repetitive contractions, which represented haustral activity; (2) low-frequency rises in the base line which represented segmental activity, and (3) monophasic progressive contractions which represented peristaltic activity (Ehrlein, Reich & Schwinger, 1982). It has not yet been established whether the occurrence of these various types of contractions is different during the formation of hard and soft faeces.

The objectives of this study were first to examine the motor patterns of the rabbit proximal colon during the production of soft and hard faeces, and secondly to clarify the way in which the mechanical activity of the colon contributes to the production of different types of faeces.

The patterns of the motor activity of the colon are documented in a film (Ehrlein, 1981).

METHODS

Definitions and abbreviations

The rabbit colon can be divided into a proximal and a distal part. The proximal colon includes three segments: the triple haustrated colon (3 h.c.) which has three rows of haustra and three taeniae; the single haustrated colon (1 h.c.) possessing a single row of haustra and a single taenia, and the fusus coli which is characterized by a thick longitudinal muscle layer and by prominent longitudinal folds of the mucosa (Fig. 1). The distal colon is devoid of sacculation.

Animals

Six domestic, cross-bred rabbits weighing 2·9–3·7 kg were used. The animals were kept under constant environmental conditions (room temperature, 20 °C; 12 hourly light/dark cycle with the light phase beginning at 8 a.m.). The animals were fed a standard laboratory diet supplemented with hay *ad libitum*. Water was available continuously.

Experimental procedures

Two groups of experiments were carried out. In group I (rabbits 1–3) the motility of the proximal and distal colon was recorded with chronically implanted, strain-gauge transducers. A catheter was inserted into the triple haustrated colon. The transit of contrast medium from the proximal to the distal colon was observed fluoroscopically. In group II (rabbits 4–6) contrast medium was infused into the single haustrated colon via an implanted catheter. The orad and aborad flow of the contrast medium was observed by fluoroscopy.

For surgical procedures the rabbits were anaesthetized with xylazine 4 mg/kg and ketamine 20 mg/kg, and given atropine sulphate 0·5 mg/kg. Anaesthesia was maintained with halothane 0·6–1·5% in O_2/N_2O (ratio 1:1) using a close-fitting, rubber face mask.

Group I. The large intestine was exposed through a mid-line abdominal incision. A Teflon catheter (0·7 × 1·5 mm), covered with a silicone tube (1·5 × 2·3 mm) and flanged with a silicone plate, was implanted in the middle of the triple haustrated colon. A small incision was made in the

antimesenteric taenia. A hypodermic needle was inserted into the bowel wall 2 cm orad of the incision. The free end of the catheter was then introduced into the bowel through the incision and pulled out through the hypodermic needle. The incision in the bowel wall was closed by a Lembert's suture. After withdrawal of the hypodermic needle the outlet of the catheter was tightly closed by a purse-string suture and covered with a small disc of polyvinyl alcohol sponge (Prosthex, Ramer Chemical Co, Ltd., Camberly, England). The disc was glued to the catheter with silicone adhesive (SV4, Bayer, Leverkusen, F.R.G.). A small piece of silver wire coated with silicone was sutured to the fusus coli as a fluoroscopic marker. Extraluminal strain-gauge transducers (type F 102, Hellige, Freiburg, F.R.G.) were sutured to the triple haustrated colon, the single haustrated colon, the fusus coli, and to the first part of the distal colon 3 cm and 8 cm distal to the fusus coli (Fig. 1). The transducers were placed along the transverse axis of the bowel to record circular muscle activity. They were prepared as previously described (Ehrlein, 1980*a*). The dimensions of the transducers were 5 × 9 mm (proximal colon) and 4 × 7 mm (distal colon). The lead wires of the transducers and the implanted catheter were pulled through a subcutaneous tunnel from the abdominal incision to the left costal flank. They were exteriorized through a small skin incision which was closed by a special plug of polyvinyl alcohol sponge (Ehrlein, 1980*a*).

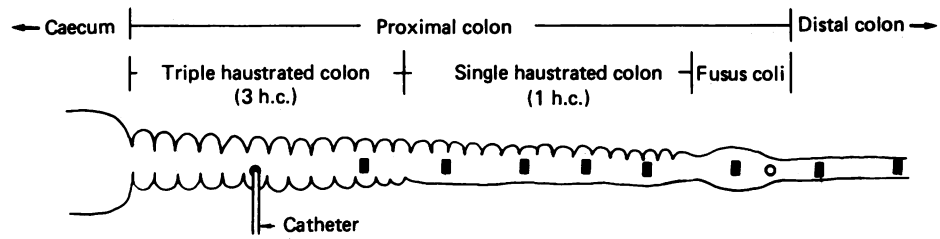

Fig. 1. Nomenclature of the rabbit colon and position of the implanted catheter and strain-gauge transducers.

Group II. A Teflon catheter covered with a silicone tube was implanted in the middle of the single haustrated colon as described for group I. Fluoroscopic markers were sutured to the bowel wall at the beginning of the single haustrated colon and at the middle of the fusus coli.

After recovery from anaesthesia the animals were fitted with protective jackets and plastic collars. The experiments were started when the rabbits had recovered from the operation and were feeding and producing faeces normally, which was usually 3–4 weeks after the operation.

The experiments were carried out either between 5 and 10 a.m. (during soft faeces formation) or between 10 a.m. and 6 p.m. (during hard faeces formation). The rabbits were positioned in a hammock. In group I experiments the strain-gauge transducers were connected with Wheatstone bridges. The amplified signals were recorded with a multichannel recorder (Hellige, Freiburg, F.R.G.) and simultaneously stored on magnetic tape via frequency modulation (Ehrlein, 1980*b*).

Radiography

Radiographic observations were made with an X-ray image-intensifier video system (Siemens, Erlangen, F.R.G.).

In group I experiments a pulpy mixture of barium was injected as a bolus of 5–8 ml into the triple haustrated colon through the implanted catheter. The passage of the contrast medium through the proximal colon was observed fluoroscopically. The transit-time through the proximal colon was defined as the period during which the injected bolus of contrast medium was carried from the middle of the triple haustrated colon to the distal side of the fusus coli. In some experiments liquid contrast medium (Conray 80 diluted with distilled water 1:1) was injected into the triple haustrated colon in addition, in order to observe retrograde movements of the haustra. Each experiment lasted 1–2 h. Recordings on video tape were made over periods of 15–20 min. In group I experiments the motility tracings were continuously filmed with a television camera. The signal from this camera was mixed with that from the X-ray television camera so that transit of the contrast medium and the motility tracings could be observed simultaneously on the monitor and stored on video tape. The advantages of this method have been previously described (Ehrlein, 1980*b*).

Typical patterns of the colonic motility were filmed using a 16 mm film monitor camera (Arriflex)

and a synchronizer (Arnold & Richter, Munich, F.R.G.). Drawings of characteristic motor patterns were prepared either from the photographs or from the video recordings using still-image play-back.

In group II experiments, liquid contrast medium (Micropaque diluted with saline 1:1) was infused into the single haustrated colon through the implanted catheter at a rate of 0·25–0·5 ml/min over a period of 5 min during periods of both soft and hard faeces production. The transit of the contrast medium was observed fluoroscopically and its passage was recorded photographically. After each experiment it was observed with which type of faeces the contrast medium was excreted, because the production of soft and hard faeces sometimes alternated sporadically. When an intermediate type of faeces was excreted the experiment was abandoned and the results excluded from the series.

Analysis

Group I. The amplitudes, the rate of progression and the duration (the time from the beginning to the end of the contraction) of the monophasic progressive contractions and of the low-frequency rises of the base line were analysed visually from the recordings, whereas the high-frequency repetitive contractions of the proximal colon and the monophasic contractions of the distal colon were analysed by means of a computer. The method of computer analysis has previously been described in detail (Ehrlein & Hiesinger, 1982). The amplitudes of contractions, the contraction time (the time from the beginning to the maximum of the contraction) and the contractile intervals (periods elapsing between the beginning of two successive contractions) were evaluated by various computer programs. The sums of the amplitudes over periods of 5 min were calculated as an index of motility.

Group II. The contrast medium which was infused into the single haustrated colon was carried partly towards the mouth and partly away from the mouth. The area of the radio-opaque digesta located proximal and distal to the infusion site was measured from photographs by planimetry in order to determine the flow in both directions.

Statistics

Mean values and standard deviations (S.D.) were calculated when the distribution of the data was symmetric. Differences of mean values were analysed using Student's t test. When the distribution of the data was asymmetric, median and range values which included 80 % of the data were evaluated. Differences of asymmetric or multimodal distributions were analysed by the U test of Wilcoxon, Mann and Whitney (Sachs, 1978).

RESULTS

Fluoroscopic observations

Hard faeces formation. During the formation of hard faeces the caecal content was forced into the triple haustrated colon by peristaltic waves which travelled from the caecal apex towards the colon. The distension of the triple haustrated colon appeared to stimulate the motor activity of the haustra. The interhaustral folds moved slowly orad towards the caecum producing a rolling movement of the haustra. The contents of the haustra were thereby transferred in the retrograde direction towards the caecum. When liquid contrast medium was injected into the triple haustrated colon through the implanted catheter, it was swept orad by the haustral activity, whereas pulpy contrast medium was retained in the triple haustrated colon and carried slowly aborad together with the colonic digesta. Annular constrictions of the bowel wall occurred near the junction of the triple and single haustrated colon with intervals between the indentations of about 17 mm. They subdivided the radio-opaque digesta into a series of segmental masses (Fig. 2*A*). The segmental indentations were sustained over a long period of time and moved slowly aborad at a rate of about 7 mm/min steadily becoming deeper. The separation of the colonic contents into faecal pellets was thereby enhanced (Fig. 2*A*). At the end of the single haustrated

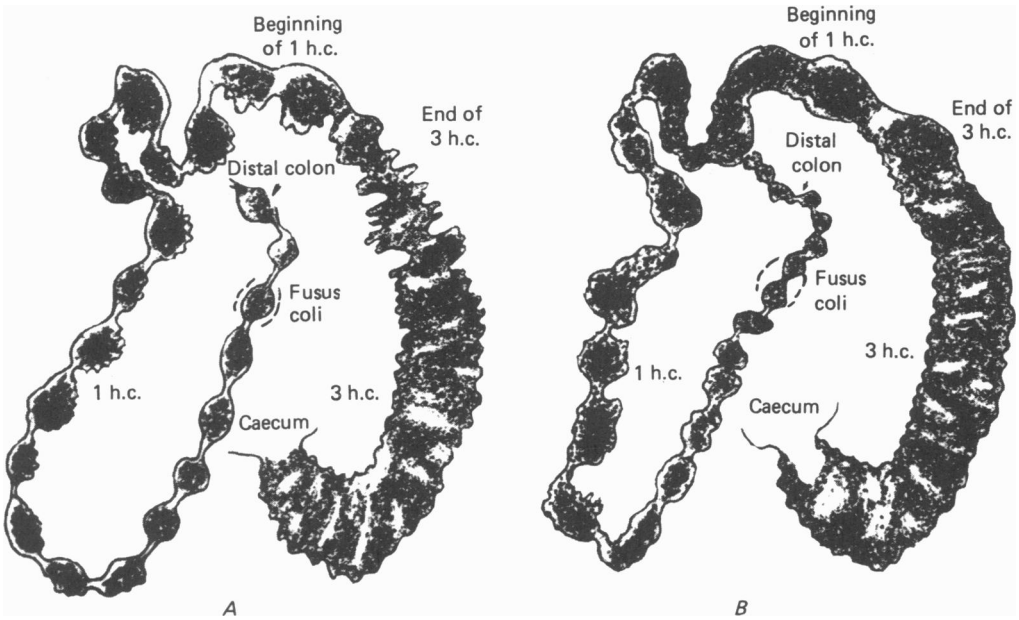

Fig. 2. Drawings of the outline of the radio-opaque contents during (*A*) hard faeces formation and (*B*) during soft faeces formation. The drawings were prepared from video recordings. Single haustrated colon, 1 h.c.; triple haustrated colon, 3 h.c.

colon the faecal pellets were completely formed. They passed through the fusus coli within 2–3 min without further alteration in shape or size.

Besides the segmental constrictions, rolling movements of the haustra were usually present in the single haustrated colon. They seemed to have two functions: they mixed the radio-opaque digesta within the segmental masses, and produced a slow retrograde transfer of liquid contents. The orad flow of liquid could be seen more clearly, when contrast medium was infused into the single haustrated colon in the group II experiments. During the period of hard faeces production (thirty-seven experiments) the liquid contrast medium was swept orad by retrograde rolling movements of the haustra. In eighteen experiments the contrast medium was carried entirely backwards towards the caecum (Fig. 3*A*). In the remaining nineteen experiments some barium ($35{\cdot}2 \pm 12\%$) accumulated at the infusion site; it was mixed with the digesta and transferred aborad by the segmental activity. Transfer of the contrast medium back from the middle of the single haustrated colon to the distal part of the triple haustrated colon lasted 2–5 min, i.e. the rate of progression was about 0·3–1 mm/s. Some barium was carried further back into the caecum but most accumulated in the triple haustrated colon and became attached to the digesta and was excreted 1–2 h later in the hard faeces.

Soft faeces formation. During the production of soft faeces the transit of contrast medium through the triple haustrated colon was similar to that during the formation of hard faeces, whereas the motility of the single haustrated colon was different. The haustral activity was very weak and the segmental constrictions less intense. Thus, the colonic content was separated into large masses instead of small pellets (Fig. 2*B*) and slowly forced towards the fusus coli by aborad movements of the segmental

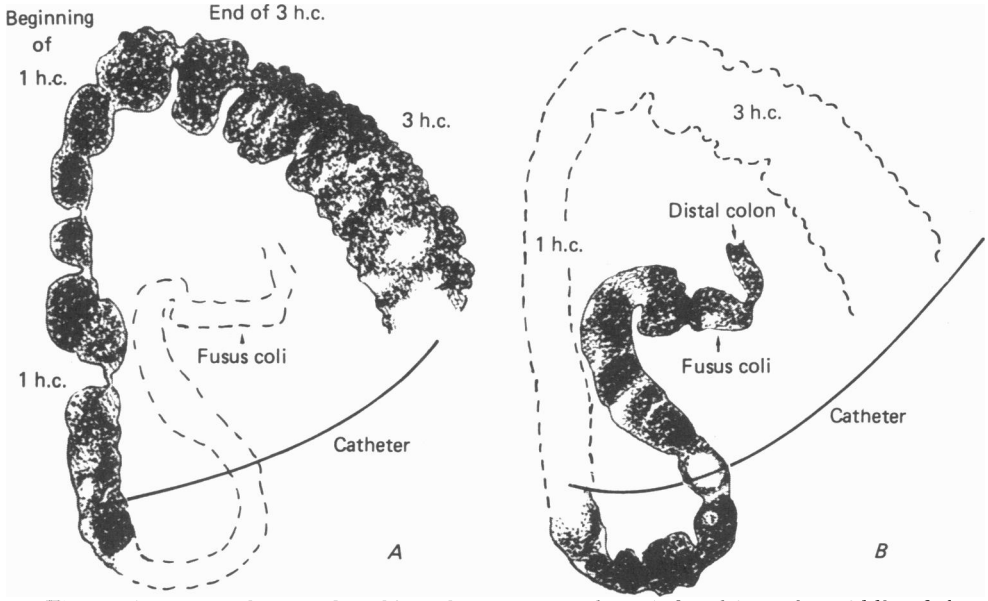

Fig. 3. *A*, retrograde transfer of liquid contrast medium infused into the middle of the single haustrated colon during the production of hard faeces. *B*, aboral transfer of liquid contrast medium infused into the single haustrated colon during the production of soft faeces. Abbreviations as in Fig. 2.

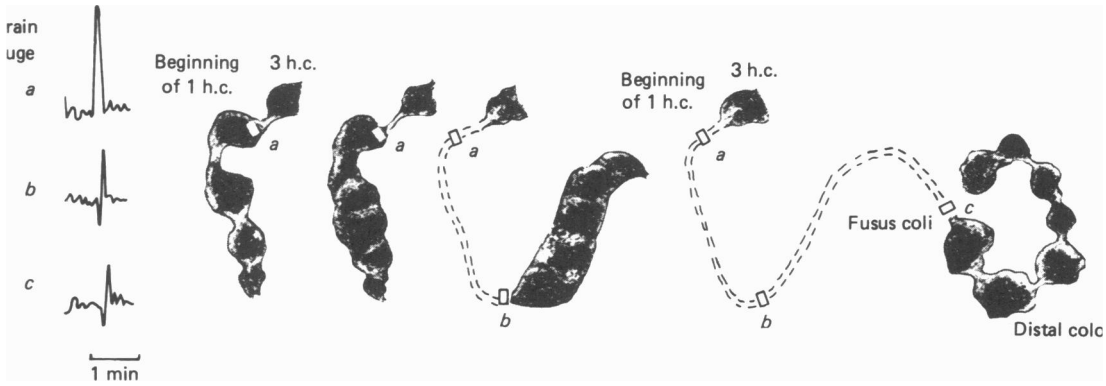

Fig. 4. Rapid transit of colonic contents by mass peristalsis migrating from the beginning of the single haustrated colon (1 h.c.) to the fusus coli during the period of soft faeces formation. *a*, *b*, *c* are sites of strain-gauge transducers.

constrictions. However, transit of the radio-opaque digesta through the single haustrated colon was often accelerated by mass movements. These occurred at irregular intervals of about 30 min and usually started near the junction between the triple and single haustrated colon (Fig. 4). They began with a disappearance of the segmental indentations and produced a progressive obliteration of the colonic lumen. Sometimes, the peristaltic waves travelled the whole length of the single haustrated colon, propelling the bowel contents ahead of them into the distal colon. After each mass peristalsis, the colonic digesta was separated again into segmental masses. Each of which was subdivided into 3–4 small faecal pellets during transit through the fusus coli or within the first few centimetres of the distal colon.

In group II experiments, in which liquid contrast medium was infused into the single haustrated colon during the period of soft faeces formation, the contrast medium usually accumulated at the infusion site and was carried slowly aborad together with the colonic content. Although the haustra moved predominantly orad, the liquid contrast medium was not delivered beyond the segmental constrictions, because the movements of the haustra were too weak. Thus, haustral activity only produced mixing of the segmental masses. In eight out of fifteen experiments the contrast medium was transported entirely aborad (Fig. 3*B*). In the remaining seven experiments, 82·5 ± 5 % of the infused contrast medium moved in the same direction but 17·5 ± 5 % was swept back towards the caecum.

TABLE 1. Transit time of radio-opaque digesta through the proximal colon during formation of hard and soft faeces in three rabbits

Rabbit	Transit time: Hard faeces (min)	Transit time: Soft faeces (min)	Length of proximal colon (cm)
A	60·4 ± 19·8 (5)	25·0 ± 12·5* (4)	38
B	47·1 ± 12·2 (8)	28·6 ± 11·5* (5)	24
C	36·3 ± 9·7 (4)	24·0 ± 16·8 (3)	32

Data are means ± S.D., numbers in parentheses indicate the number of experiments. * $P < 0·05$.

Transit time. The transit time of the radio-opaque digesta through the proximal colon was measured in three rabbits during periods of hard faeces formation (seventeen experiments) and during periods of soft faeces formation (twelve experiments). In two rabbits the transit time in the proximal colon was significantly longer during the production of hard faeces compared with that during the production of soft faeces (Table 1). The mean transit velocities were 0·7 ± 0·3 cm/min during formation of hard faeces and 1·6 ± 0·8 cm/min during formation of soft faeces.

Recordings of motility

Hard faeces formation. During the production of hard faeces the motor activity of the proximal colon was enhanced (Fig. 5*A*). Three types of contraction were identified from the tracings: (1) high-frequency repetitive contractions; (2) low-frequency rises in the base line, and (3) monophasic progressive contractions. Simultaneous fluoroscopy showed that the high-frequency repetitive contractions represented haustral activity, whereas the rises in the base line were caused by segmental constrictions. The segmental constrictions persisted over long periods of time and migrated slowly aborad. The monophasic progressive contractions occurred very seldom and represented peristaltic waves. They could be identified on the tracings as single monophasic waves of greater amplitude which occurred successively at adjacent recording sites.

The motor activity of the distal colon consisted of monophasic waves which lasted longer than the high-frequency repetitive contractions of the proximal colon (Fig. 5*A*). During production of hard faeces the motor activity of the distal colon was relatively weak. The first 3 cm of the distal colon showed motor patterns characteristic of both the proximal colon (low-frequency rises in the base line and high-frequency repetitive contractions) and the distal colon (monophasic waves of longer duration), revealing a transitional zone of motor activity.

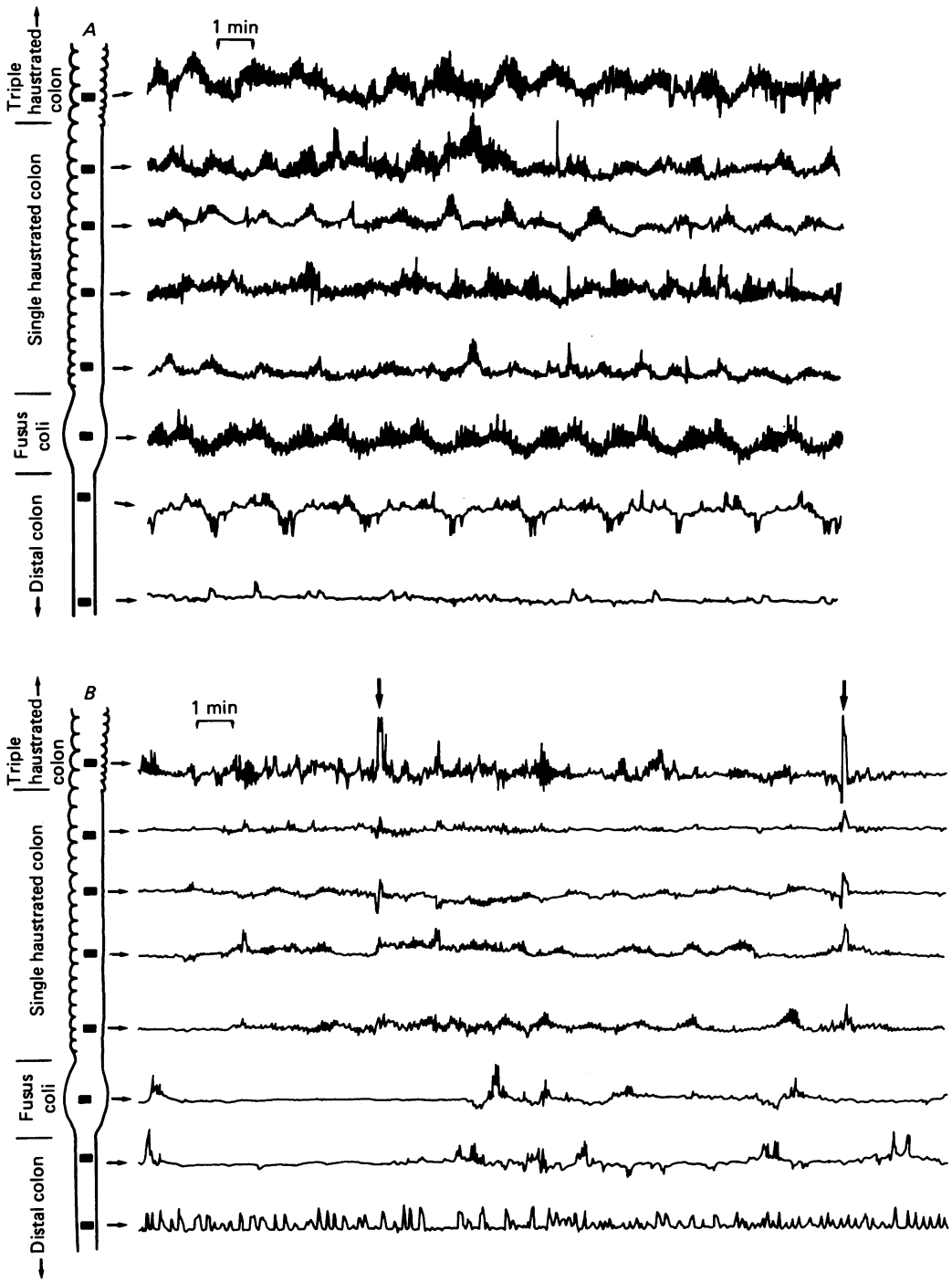

Fig. 5. Motility tracings of the proximal and distal colon during hard faeces formation (*A*) and during soft faeces formation (*B*). The motor activity of the proximal colon was enhanced during the production of hard faeces, whereas the motor activity of the distal colon was enhanced during the production of soft faeces. Arrows indicate mass peristalsis.

Soft faeces formation. During the production of soft faeces motility of the distal colon was enhanced, whereas that of the proximal colon was reduced (Fig. 5*B*). In the proximal colon, high-frequency repetitive contractions were sparse, and the amplitude of the base-line fluctuations was low. In contrast, monophasic progressive contractions which represented mass peristalsis often appeared on the tracings (Fig. 5*B*). Contractions of the distal colon consisted of monophasic waves which occurred at a higher frequency than those during hard faeces formation.

A visible alteration of the motor activity occurred during the transitional period between the production of soft and hard faeces (Fig. 6).

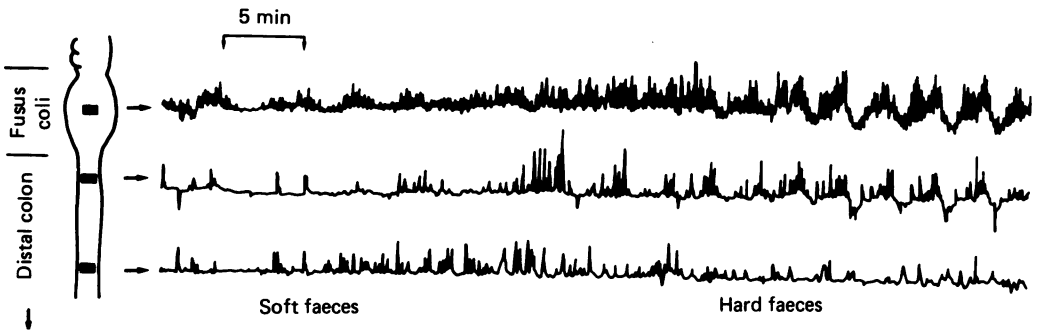

Fig. 6. Motility recordings of fusus coli and distal colon during a transitional period between soft and hard faeces formation.

Analysis of the motor activity

Differences between hard and soft faeces formation in the proximal colon

High-frequency repetitive contractions. The motility index and the contractile intervals of the high frequency repetitive contractions of the proximal colon (fusus coli) were analysed by computer over a 25 h period during the production of both soft and hard faeces. The total number of the repetitive contractions was about four times greater during hard faeces formation than during soft faeces formation (Table 2). The histogram of the contractile intervals showed a multimodal distribution. During the production of hard faeces, 85 % of the repetitive contractions had short contractile intervals ($3{\cdot}6 \pm 0{\cdot}4$ s), whereas during the production of soft faeces only 41 % of the repetitive contractions occurred at short intervals ($3{\cdot}8 \pm 0{\cdot}6$ s). The remaining 59 % of the repetitive contractions had contractile intervals ranging between 5·5 and 20 s (Table 2). The multimodal distribution of the contractile intervals was significantly different between the periods of hard and soft faeces formation (*U* test of Wilcoxon, Mann & Whitney). The motility index of the repetitive contractions was also significantly higher during the formation of hard faeces (Table 2).

Low-frequency rises of the base line. Rhythmic rises of the base line were present during the production of both soft and hard faeces. The mean duration of the base-line fluctuations was 131 ± 47 s; this corresponds to an average rate of 4·6 contractions/10 min. Neither the rate or duration of the base-line fluctuations differed significantly between periods of hard and soft faeces formation. However, the amplitudes of the base-line fluctuations were significantly larger during the production of hard faeces (Table 2).

Monophasic progressive waves. Strong monophasic contractions which occurred successively at adjacent recording sites could be clearly identified from the tracings during both the production of soft faeces (seventy events accompanied with mass movements) and hard faeces (twenty-six events accompanied by propulsion of gas). The average incidence of the monophasic progressive waves was 0·5 contractions/h during formation of hard faeces and 2·2 contractions/h during the production of soft faeces (Table 2). The mean duration of the monophasic progressive waves was $9{\cdot}7 \pm 2{\cdot}8$ s and $5{\cdot}5 \pm 1{\cdot}2$ s during the production of soft and hard faeces, respectively. The rate of progression was significantly lower during the period of soft faeces formation ($1{\cdot}3 \pm 0{\cdot}6$ cm/s) compared to the period of hard faeces formation ($3{\cdot}2 \pm 1{\cdot}2$ cm/s).

TABLE 2. Differences of the motor activity of the proximal and distal colon during the production of hard and soft faeces in three rabbits

	Hard faeces (mean ± S.D.)		Soft faeces (mean ± S.D.)	
Proximal colon				
Repetitive contractions				
No. of contractions/25 h	18848		4645	
Contractile intervals (s)	$3{\cdot}6 \pm 0{\cdot}4$	(85%)	$3{\cdot}8 \pm 0{\cdot}6$	(41%)
	$7{\cdot}0 \pm 0{\cdot}7$	(15%)	$7{\cdot}1 \pm 0{\cdot}9$	(22%)
			9–20	(37%)
Motility index	11761 ± 3298*	(300)	2350 ± 1656	(300)
Rises of base-line amplitudes (mm)	$9{\cdot}4 \pm 2{\cdot}8$*	(1856)	$3{\cdot}2 \pm 2$	(3108)
Monophasic progressive waves				
Incidence/h	0·5	(26)	2·2	(70)
Duration (s)	$5{\cdot}5 \pm 1{\cdot}2$*	(26)	$9{\cdot}7 \pm 2{\cdot}8$	(70)
Rate of progression (cm/s)	$3{\cdot}2 \pm 1{\cdot}2$	(15)	$1{\cdot}3 \pm 0{\cdot}6$	(70)
Distal colon				
Monophasic contractions motility index	1032 ± 501*	(300)	2309 ± 1311	(300)
	Median	Range	Median	Range
Contractile intervals (s)	28·3*	7·7–91·4	15·6	7·9–42·1

* $P < 0{\cdot}001$, numbers in parentheses indicate the number of data. The percentage incidence is shown.

Differences between hard and soft faeces formation in the distal colon

The repetitive contractions of the proximal colon and the monophasic contractions of the distal colon showed large differences in relation to both contractile intervals and duration of contraction. When the repetitive contractions of the proximal colon occurred at maximal frequency, the average interval was $3{\cdot}6 \pm 0{\cdot}4$ s (period of hard faeces formation). In the distal colon the intervals between the monophasic waves were about 3·4 times longer (period of soft faeces formation: median 15·6 s, range 7·9–42·1 s) than those in the proximal colon (Table 2). The repetitive contractions in the proximal colon persisted for $1{\cdot}6 \pm 0{\cdot}5$ s, whereas the monophasic waves in the distal colon were significantly more protracted, lasting up to 7·9 s.

DISCUSSION

In the present study distinct differences in colonic motility during the formation of soft and hard faeces were found. The differences were most pronounced in the single haustrated colon. When hard faeces were produced the motor activity of the single haustrated colon was enhanced. It consisted of segmental contractions and of haustral activity. The segmental contractions separated the digesta into faecal pellets and forced them slowly aborad. At the same time, the movements of the haustra carried liquid content back towards the caecum. It is therefore likely that a mechanical separation of liquid and solid was thereby produced. In contrast, the segmental and haustral activity of the single haustrated colon was relatively weak during the formation of soft faeces, whereas the occurrence of mass peristalsis was increased. The caecal content passed through the proximal colon more rapidly, without signs of mechanical separation into liquids and solids. The faecal masses were divided into small pellets in the fusus coli and in the most proximal part of the distal colon. This process was accompanied by an increase in motility in the distal colon. These results support the concept that hard faeces are produced by a mechanical separation of liquids and solids during the transport of digesta through the proximal colon (Pickard & Stevens, 1972; Björnhag, 1972, 1981*a*). Our findings also confirm Björnhag's observation (1981*b*) that liquid contrast medium was carried from the single haustrated colon towards the caecum during the formation of hard faeces.

In our study it has been more difficult to prove that the contrast medium passes down the gastrointestinal tract in the usual direction, during soft faeces formation, than to demonstrate the orad flow during the production of hard faeces. The single haustrated colon seems to be very sensitive to the implantation of a catheter. Although the catheter was very small, colonic motility was disturbed, appetite was reduced, and an intermediate type of faeces (neither soft nor hard) was often produced for some weeks. The animals then recovered and produced normal soft and hard faeces (except for one rabbit in which soft faeces were no longer excreted in a definite circadian rhythm but were produced sporadically). In some experiments, the formation of soft faeces was interrupted by the infusion of the liquid contrast medium. In each of these experiments the contrast medium was excreted later in hard faeces. Afterwards the production of soft faeces continued. Björnhag (1972) and Clauss (1978) supposed that net secretion of water into the single haustrated colon occurred during the formation of hard faeces. It is likely that liquid stimulates retrograde movements of the haustra and that a net flux of water into the single haustrated colon is accompanied by an increase of the haustral activity during formation of hard faeces. The change in composition occurs mainly in the single haustrated colon (Snipes, Clauss, Weber & Hörnicke, 1982). From our results it is also evident that the proximal colon and especially the single haustrated colon, is the most important site for the production of these different types of faeces in the rabbit.

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