Gastrointestinal Motility

H. J. Ehrlein and M.Schemann

1. Motility of the stomach

Anatomic regions of the stomach are the fundus, corpus (body), antrum and pylorus. The functional regions of the stomach do not correspond to the anatomic regions. Functionally, the stomach can be divided into the gastric reservoir and the gastric pump (Fig. 1). The gastric reservoir consists of the fundus and corpus. The gastric pump is represented by the area at which peristaltic waves occur: it includes the distal part of the corpus and the antrum. Due to different properties of the smooth muscle cells the gastric reservoir is characterised by tonic activity and the gastric pump by phasic activity.
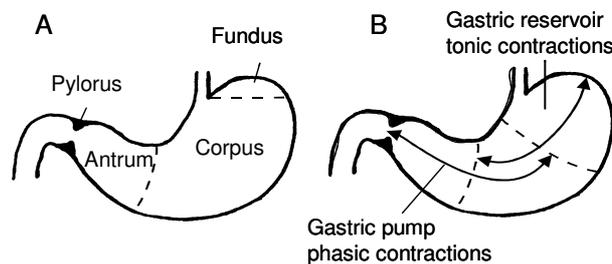

Figure 1. The stomach can be divided into three anatomic **(A)** and two functional regions **(B)**

1.1 Function of the gastric reservoir

At the beginning of the 20th century it was already observed that with increasing volume of the stomach the internal pressure of the stomach increases only slightly. In dogs, for instance, the increase in pressure is only 1.2 cm of water/100 ml volume. The small increase in gastric pressure indicates that the stomach does not behave like an elastic balloon but that it relaxes as it fills. Three kinds of *gastric relaxation* can be differentiated: a receptive, an adaptive and a feedback-relaxation of the gastric reservoir. The receptive relaxation consists of a brief relaxation during chewing and swallowing. The stimulation of mechano-receptors in the mouth and pharynx induces vago-vagal reflexes which cause a relaxation of the gastric reservoir (Fig. 2). By this receptive relaxation the stomach is prepared to receive a bolus of food. When the stomach is filled with digesta, mechano- and/or chemoreceptors are stimulated which elicit gastro-gastric reflexes and thus an adaptive relaxation (Fig. 2). This regulation provides a prolonged storage of the digesta until they are sufficiently broken down for emptying into the duodenum. Among others Gastrin, which stimulates the secretion of gastric juice, causes an additional relaxation of the gastric reservoir. This hormonal control stimulates an increased volume in the stomach for the secreted gastric juice without increase in intraluminal pressure. A further reflex regulation of the gastric reservoir is induced by nutrients of the small intestine (Fig. 2).

This feedback-relaxation of the stomach and the associated prolonged storage of digesta are a precondition that gastric emptying is adapted to the process of digestion and absorption of nutrients in the small intestine. Because both the gastric reservoir and the gastric pump are involved in the feedback regulation, this control mechanism is described in detail in chapter 1.4.
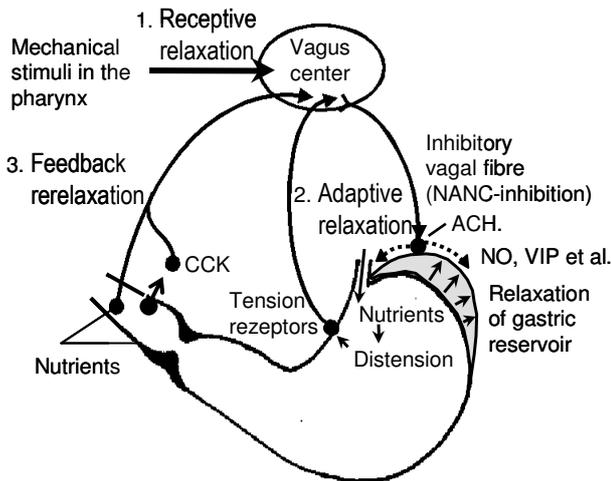
Figure 2. The relaxation of the gastric reservoir is mainly regulated by reflexes. Three kinds of relaxation can be differentiated: the receptive, adaptive and feedback-relaxation. The inhibitory vagal fibres releasing ACH activate inhibitory enteric pathways (dotted arrows) that release NO, PACAP, VIP and/or ATP in order to relax the muscle

The receptive, adaptive and feedback-relaxation of the stomach are mediated by non-adrenergic, non-cholinergic mechanisms (called NANC-inhibition) as well as by reflex chains involving release of norepinephrine from sympathetic fibers. Mediators for NANC inhibition are nitric oxide (NO), Pituitary adenylate cyclase activating peptide (PACAP), vasocative intestinal peptide (VIP) and adenosine triphophate (ATP), all of which are released from motor pathways in the enteric nervous system. Vago-vagal reflexes use enteric pathways to modulate smooth muscle activity. Thus excitatory vagal pathways innervate excitatory enteric pathways that release acetylcholine (Ach) in order to contract the muscle while inhibitory vagal pathways innervate inhibitory enteric pathways that release the NO, PACAP, VIP and/or ATP in order to relax the muscle. In each case vagal efferents activate enteric motor pathways by the release of acetylcholine which in turn activates nicotinic receptors abundantly present on enteric neurones. This enables the few vagal efferent fibers to specifically evoke excitation or inhibition by using the enteric nervous system as a relay station (Fig.2).

The gastric reservoir has functions to store and to evacuate digesta. The emptying of the reservoir is caused by two mechanisms: by a tonic contraction of the reservoir and by peristaltic waves moving over the distal part of the gastric corpus. They represent the pump of the gastric reservoir (Fig. 3). Both the peristaltic waves and the tonic contractions of the reservoir are stimulated by cholinergic enteric neurones that are under modulatory vagal tone In the region of the gastric corpus the peristaltic waves only produce a small circular constriction. Thus they mix and evacuate only the superficial layer of the digesta diluted by gastric juice while in the centre of the gastric reservoir the pH remains high and the digestion of starch by amylase continues.
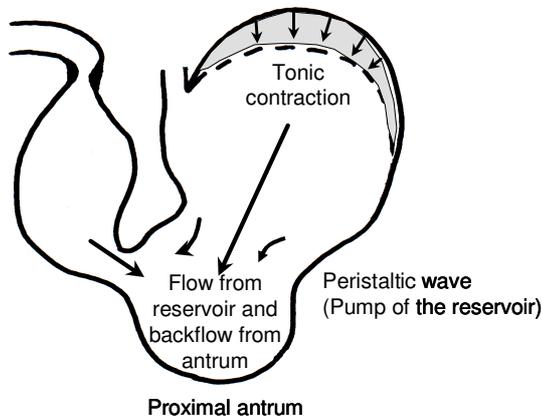

Figure 3. The transport of digesta from the gastric reservoir into the antral pump is caused by two mechanisms: tonic contractions and peristaltic waves in the region of the gastric corpus.

Table 1. Frequency and propagation velocity of contraction waves in stomach and small intestine in the dog, human, pig, sheep and rabbit.

-	Maximal frequency [contractions/min]	Velocity [cm/sec]
Stomach		
Dog	5,2	0.8-1.1
Rabbit	4.6	0.4-0.5
Pig	3.3	–
Sheep	5.4	–
Human	3	
Small intestine		
Dog		
Duodenum	15.8–17.8	7-12
Jejunum	17–17.7	4.7
Ileum	13.3–13.8	0.7-0.8
Pig		
Duodenum	17–18	8
Jejunum	15	5.6
Ileum	11	0.5
Sheep		
Ileum	14.4–14.8	0.4
Human		
Duodenum	11	–

1.2 Function of the gastric pump

The main feature of the gastric pump is the peristaltic wave. It originates at the proximal stomach and propagates to the pylorus. The peristaltic waves are based on electrical waves originating in the gastric wall. In the wall of both the stomach and small intestine, there is a network of interstitial cells – called interstitial cells of Cajal (ICC). These interstitial cells produce electrical *pacesetter potentials* due to oscillations in their membrane potential. The pacesetter potential of the ICCs drive electrical events in the smooth muscle cells where they are reflected by *slow waves*. The *pacesetter potentials* and *slow waves* start in the proximal stomach and move aborally along the syncitium of the smooth muscle cells. The frequency of the pacesetter potentials differs among species. The pacesetter potentials determine the maximal frequency and the propagation velocity of the peristaltic waves (Table 1). However, the pacesetter potentials do not cause contractions by themselves: they are always present even when the stomach lacks any contractile activity. Contractions only occur, when excitatory neurotransmitters, one of the most prominent being acetylcholine, are released. Acetylcholine opens calcium channels during the maximum of the pacesetter potentials, so that influx of calcium into the smooth muscle cells occurs. The influx of calcium induces the electro-mechanical coupling. It is associated with the occurrence of *spike potentials.* The release of acetylcholine and thus the stimulation of gastric motility occurs by cephalic and gastric reflexes: they are elicited by mechano-receptors of the mouth during the ingestion of food and by mechano- and/or chemoreceptors receptors in the stomach. In the region of the gastric corpus the peristaltic waves are shallow; they represent – as mentioned above – the pump of the gastric reservoir. When the peristaltic wave reaches the antrum, the circular constriction becomes deeper. The emptying mechanism of the antral pump can be divided into three phases: 1) a **phase of propulsion**, 2) a **phase of emptying and mixing**, and 3) a **phase of retropulsion and grinding** (Fig. 4). Due to the regularly occurring pacesetter potentials these phases occur cyclically. When the peristaltic wave moves over the proximal antrum the previously contracting terminal antrum relaxes. Therefore chyme is propelled into the distal (or terminal) antrum (*phase of propulsion*).
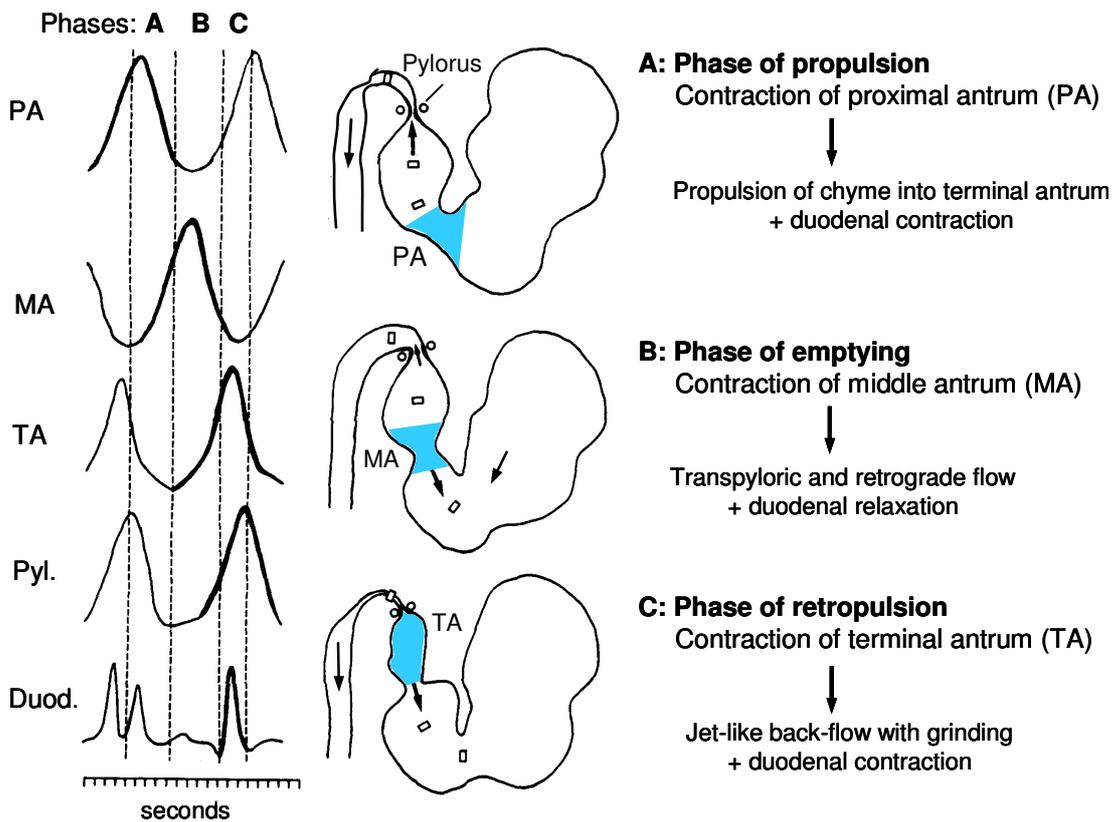
Phases: **A B C**

PA

MA

TA

Pyl.

Duod.

seconds

A: Phase of propulsion
Contraction of proximal antrum (PA)

↓

Propulsion of chyme into terminal antrum
+ duodenal contraction

B: Phase of emptying
Contraction of middle antrum (MA)

↓

Transpyloric and retrograde flow
+ duodenal relaxation

C: Phase of retropulsion
Contraction of terminal antrum (TA)

↓

Jet-like back-flow with grinding
+ duodenal contraction

Pylorus

PA

MA

TA

Figure 4 The function of the gastric pump can be differentiated into three phases:
A: phase of propulsion during propagation of the peristaltic wave over the proximal antrum,
B: phase of emptying during propagation of the peristaltic wave over the middle antrum,
C: phase of retropulsion and grinding during propagation of the peristaltic wave over the terminal antrum

When the peristaltic wave moves over the middle of the antrum the pylorus opens and duodenal contractions are inhibited; thus, small amounts of gastric chyme are delivered across the pylorus into the duodenum. During this *phase of emptying and mixing* the peristaltic waves are relatively far away from the pylorus, i.e. the gastric chyme is not forced into the duodenum by pressure but is swept into the small intestine by the peristaltic wave. This mechanism of the antral pump is associated with a sieving effect. Because liquids flow more rapidly than viscous and solid materials liquids with small suspended particles are swept across the pylorus into the duodenum whereas the viscous and solid mass of the chyme are retained in the stomach (Fig. 5).
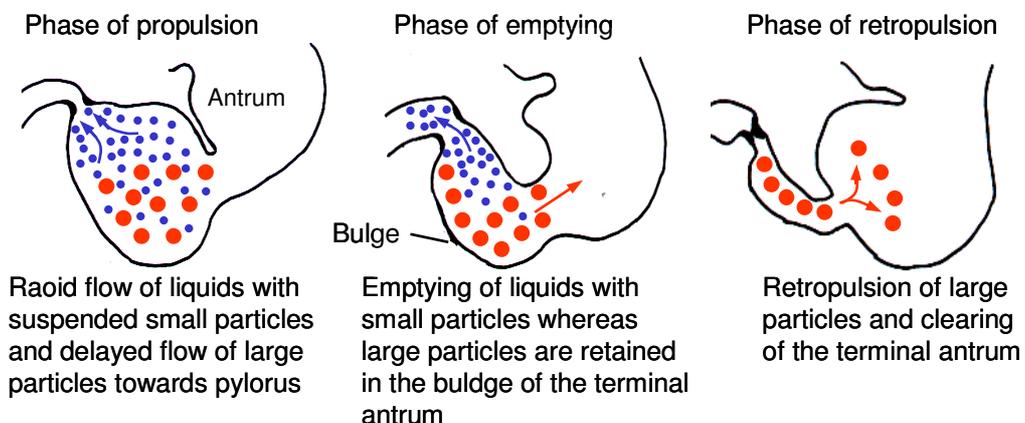
Phase of propulsion

Antrum

Phase of emptying

Bulge

Phase of retropulsion

Raoid flow of liquids with
suspended small particles
and delayed flow of large
particles towards pylorus

Emptying of liquids with
small particles whereas
large particles are retained
in the buldge of the terminal
antrum

Retropulsion of large
particles and clearing
of the terminal antrum

Figure 5. Liquids and small particles leave the stomach more rapidly than larger particles.
This discrimination is called „sieving function".

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Usually, the peristaltic waves do not occlude the lumen of the middle antrum. Therefore, parts of the chyme flow across the central opening of the peristaltic wave retrograde into the relaxing proximal antrum (Fig. 4). In this way the phase of emptying is associated with mixing of the gastric chyme. At the same time the subsequent peristaltic wave proceeds along the gastric body sweeping chyme into the proximal antrum. Thus chyme of the gastric body and chyme of the middle antrum accumulate in the relaxed proximal antrum (Figs. 3, 4). During the contraction of the terminal antrum the pylorus closes and the transpyloric flow is stopped. The chyme present in the terminal antrum is forced retrograde across the central opening of the peristaltic wave into the relaxing middle antrum (Fig. 4). This jet-like retropulsion causes a forceful mixing of the chyme associated with grinding of particles (Fig. 6). Therefore the contraction of the terminal antrum represents the *phase of retropulsion and grinding*. In herbivores grinding of the fibre-rich plants is limited. These animals produce large amounts of gastric juice and thereby deliver fibre together with liquid across the pylorus into the duodenum.
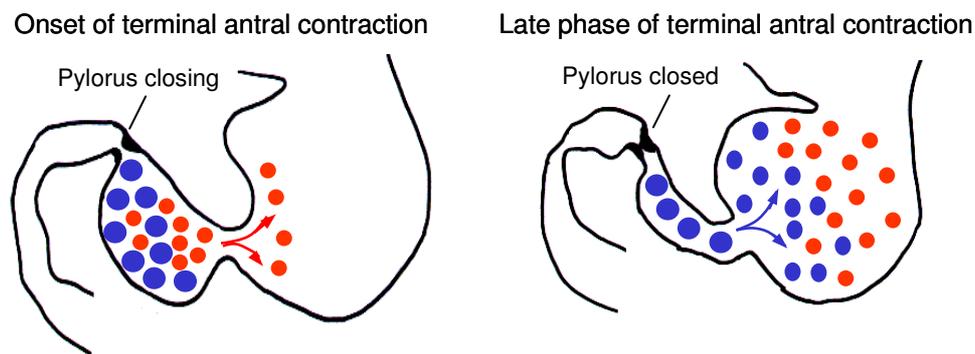
Onset of terminal antral contraction　　Late phase of terminal antral contraction

Pylorus closing　　　　　　　　　　Pylorus closed

Figure 6. Grinding of solid particles is caused by a jet-like retropulsion through the small orifice of the terminal antral contraction. The contraction of the terminal antrum is forceful and occludes the lumen.

The motility of the duodenum is strongly related to that of the stomach. This relationship is called the "antro-duodenal co-ordination". Because the pylorus is an electric isolator, the electric and thus the peristaltic waves of the stomach end at the pylorus. The pacesetter potentials of the duodenum are characterised by a higher frequency compared with that of the stomach; consequently the duodenum can contract three to four times during an antral wave (Fig. 7). During the emptying phase of the stomach the duodenal contractions are inhibited and the duodenal bulb relaxes. This is designated as antro-duodenal coordination (Figs. 4, 7). A first duodenal contraction usually occurs during the gastric phase of retropulsion, i.e. during the contraction of the terminal antrum associated with pyloric closure (Figs. 4, 7). A second duodenal contraction can occur during the gastric phase of propulsion. The duodenal contractions are peristaltic waves starting at the bulb and forcing the emptied chyme distally like a conveyor belt; however, after a nutrient meal the peristaltic waves are stopped at the proximal duodenum by additional stationary segmenting contractions.

1.3　Gastric emptying

The complex functions of the gastric reservoir and the gastric pump indicate, that gastric emptying depends on several factors (Fig. 8). The relaxation of the reservoir, the depth of the constriction of the antral waves, the degree of pyloric opening, the receptive relaxation of the duodenal bulb and the contractile pattern of the duodenum play an important role. A long lasting relaxation of the reservoir (Fig. 8, No. 6a) and a shallow peristaltic wave of the gastric corpus (Fig. 8, No. 6b) are a precondition for delayed gastric emptying, whereas a tonic contraction of the reservoir (Fig. 8, No. 1a) and a deep peristaltic wave of the gastric corpus (Fig. 8, No. 1b) contribute to an accelerated gastric emptying. A forceful peristaltic wave of the antrum associated with a deep constriction (Fig. 8, No. 2) causes an enhanced propulsion and flow of chyme across the pylorus during the phase of emptying, whereas a

lower constriction of the antral wave reduces propulsion and increases retropulsion (Fig. 8, No. 7). During the phase of emptying, the opening of the pylorus varies due to modulation of the tonic activity (Fig. 8, No. 3 and 8). Thereby the resistance of the gastric outlet and consequently the transpyloric flow are modulated. A receptive relaxation of the duodenal bulb (Fig. 8, No. 4) reduces the resistance elicited from the small intestine, whereas a narrow duodenum (Fig. 8, No. 9) enhances the resistance. Peristaltic waves of the duodenum forcing the emptied chyme aborally (Fig. 8, No 5), additionally support gastric emptying, while segmenting contractions (Fig. 8, No. 10) enhance the duodenal resistance and inhibit the transpyloric flow. The motility of the stomach can be stimulated by hormones or chemical drugs. However, an increase in gastric emptying only occurs when the co-ordination between the reservoir, pump and duodenal motility is preserved. At present, an effective stimulation of gastric emptying can be obtained by motilides like Erythromycin which enhances gastric contractions via motilin receptors.
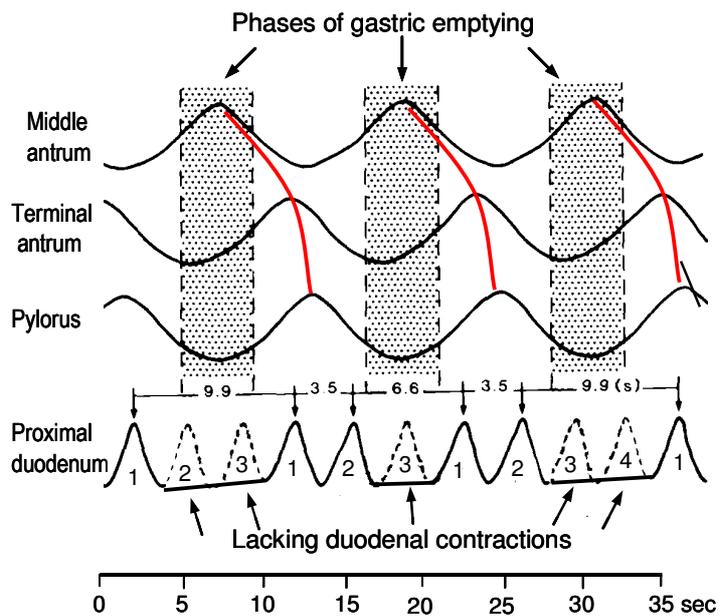

Figure 7. Antro-duodenal coordination: Because of different frequencies between antral and duodenal contractions, the duodenum can contract three to four times during an antral wave (red lines). The contractions of the proximal duodenum cease during the phases of gastric emtying. The first duodenal contraction occurs during the gastric phase of retropulsion, the second contraction occurs during the phase of propulsion (see Fig. 4)
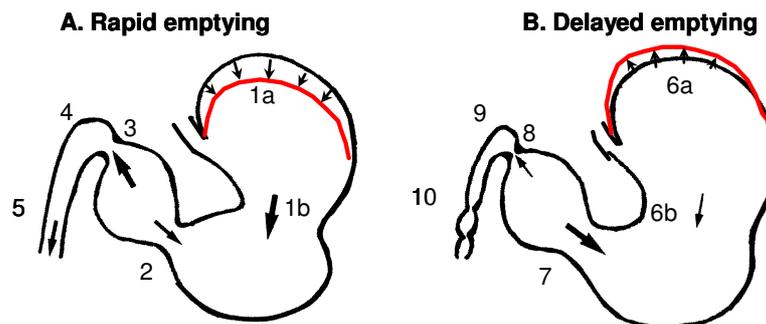

Figure 8. Several factors of gastric and duodenal motility cooperate and modulate gastric emptying. **A. Rapid emptying** of a non-caloric viscous meal of cellulose gum: tonic contractions of the reservoir (1a) and deep peristaltic waves along the gastric body (1b) produce rapid delivery of chyme to the antrum.Deep constriction of the antral waves (2) cause forceful propulsion. A wide opening of the pylorus (3) and a duodenal receptive relaxation (4) result in large transpyloric flow. Peristaltic duodenal contractions (5) produce rapid transfer of chyme to the jejunum. **B. Delayed emptying** of a nutrient meal due to feedback inhibition: prolonged relaxation of the reservoir (6a) and shallow peristaltic waves along the gastric body (6b) cause small flow of chyme to the antrum. Shallow antral waves (7) produce low propulsion and enhanced retropulsion. A small pyloric opening (8), a small duodenal relaxation (9) and segmenting duodenal contractions (10) cause large resistances and consequently a small transpyloric flow.

1.4   Regulation of gastric motility and emptying

The motility and emptying of the stomach are modulated by various control mechanisms, which are elicited either in the stomach or in the small intestine. The main function of the stomach is to store the chyme until it is sufficiently broken down to small particles and liquid. In contrast, the regulation induced by the small intestine takes care that gastric emptying is sufficiently reduced and adapted to the intestinal processes of digestion and absorption.

Regulation elicited from stomach

The functions of the gastric reservoir and the antral pump require a co-ordination. This is provided by gastro-gastric reflexes. The filling and distension of the reservoir elicit excitatory reflexes stimulating antral contractions (Fig. 9). In this way the antral pump is immediately activated when food enters the stomach. In contrast, a distension of the antrum induces inhibitory reflexes resulting in enhanced and prolonged relaxation of the gastric reservoir (Fig. 9). Thus these gastro-gastric reflexes provide a balance between the functions of the gastric reservoir and the antral pump.
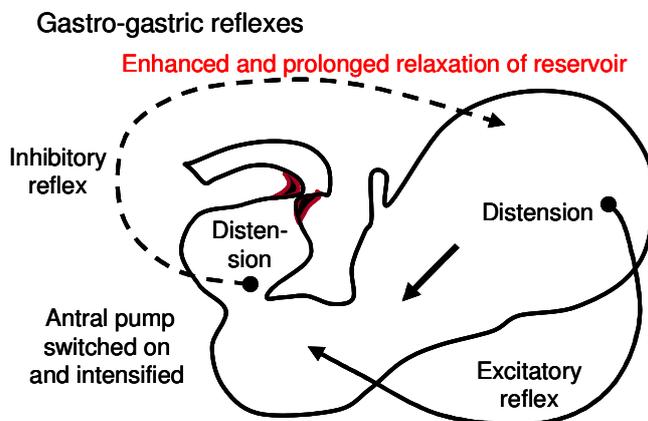
Gastro-gastric reflexes

Enhanced and prolonged relaxation of reservoir

Inhibitory reflex

Disten-sion

Distension

Antral pump switched on and intensified

Excitatory reflex

Figure 9 Gastro-gastric reflexes provide balance between gastric reservoir and antral pump. Distension of the reservoir stimulates antral contractions. Distension of the antrum enhances and prolongs relaxation of the reservoir.

The activity of the pyloric sphincter is modulated by reflexes originating from the antrum and duodenum. A contraction of the middle antrum elicits a descending inhibitory reflex causing pyloric relaxation via the release of NO and VIP (Fig. 10). On the other hand, duodenal stimuli like hydrochloric or oleic acid induce an ascending excitatory reflex which causes frequent contractions of the pyloric sphincter associated with an increase in tone (Fig. 10). The duodenal excitatory reflex contributes to prevent duodeno-gastric reflux (Fig. 11). Figure 11 further shows that the pyloric sphincter can contract either in the antral or the duodenal rhythm.

Descending inhibitory reflex causing pyloric relaxation
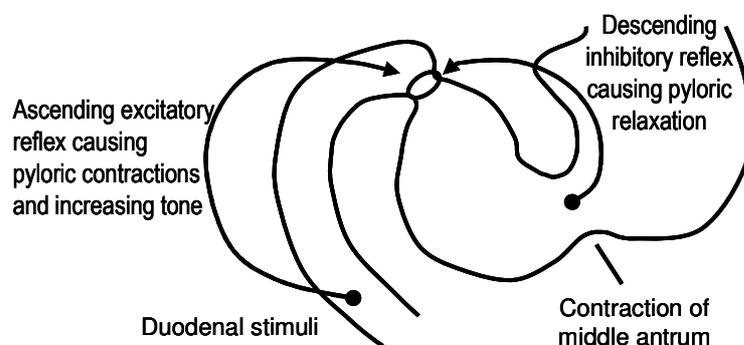
Ascending excitatory reflex causing pyloric contractions and increasing tone

Figure 10 Pyloric activity is modulated by antral inhibitory and duodenal excitatory reflexes

Duodenal stimuli

Contraction of middle antrum

Gastric emptying of liquids starts immediately after eating. After an initial rapid emptying of liquids, the emptying rate decreases so that the emptying pattern of liquids is exponential. (Fig. 12). Gastric emptying of viscous content is slower and is mainly linear. The slower emptying rate is partly caused by the enhanced resistance to flow of the viscous chyme. Additionally, with increasing viscosity the depth of the peristaltic constrictions is diminished and consequently the propulsion is reduced. After a fibre-rich or solid meal gastric emptying only starts after a lag phase because the solid particles have to sufficiently broken down before they can be evacuated (Fig. 12).
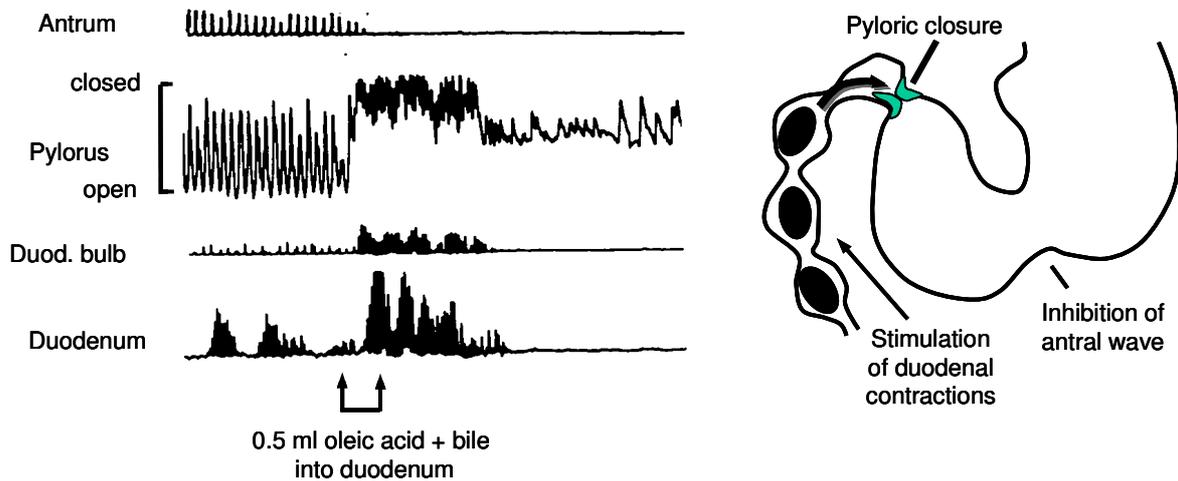

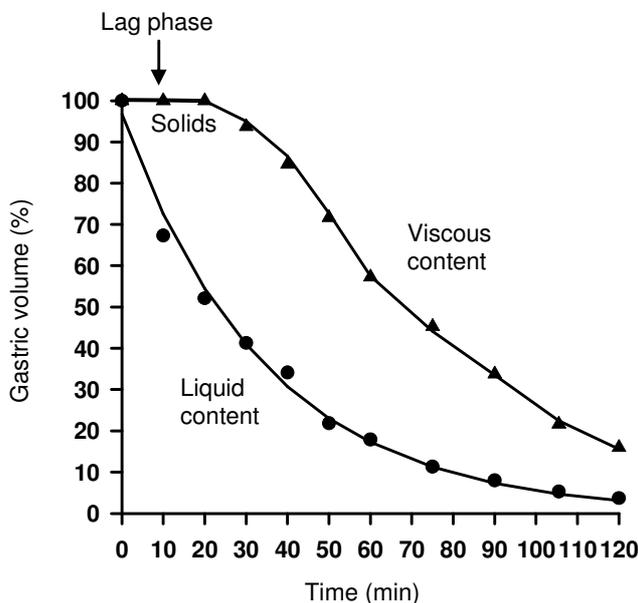**Figure 11** An additional function of the pyloric sphincter is to prevent duodeno-gastric reflux

Figure 12. Solids and liquids of the gastric chyme are emptied with different velocity. Emptying of liquids is exponential, emptying of large solid particles only begins after sufficient grinding (lag phase). Afterwards the viscous chyme is mainly emptied in a linear fashion.

Regulation elicited from small intestine

Gastric emptying is inhibited by nutrients entering the small intestine. This regulation – designated as **feedback control** – is already induced in the duodenum. It is called the "duodenal brake". However, the jejunum (jejunal brake) and ileum (ileal brake) , i.e. the entire small intestine is involved in the feedback regulation of gastric emptying. The inhibition of gastric

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emptying is caused by all the factors described above which influence the emptying mechanism (Fig. 8). The modulation of gastric motility becomes clearcut by comparison of gastrointestinal motor patterns after a non-caloric meal of cellulose gum and after a nutrient meal (Fig. 13). The feedback-inhibition of gastric emptying is elicited by various stimuli (Fig. 14). Hydrochloric acid, enhanced or diminished osmolality of the chyme, and an increased amount of nutrients entering the small intestine reduce the rate of gastric emptying. The regulation is caused by both entero-gastric neural reflexes and the release of intestinal hormones. In the feedback-regulation due to neural reflexes the vagus has a dominant role. Receptors for glucose, osmolality, hydrochloric acid, amino acids and long chain fatty acids could be identified by measuring the spike activity of afferent vagal fibres. However, these receptors are not morphologically distinct structures, but the afferent vagal fibres themselves have receptor function. The inhibition of gastric emptying is mainly induced by nutrients which are hydrolysed and ready for absorption. Besides reflexes intestinal hormones are also involved in the feedback regulation. One of the most important hormone is cholecystokinin (CCK), which is released by luminal hydrochloric acid, amino acids and long chain fatty acids from I-cells of the intestinal epithelium (Fig. 14). The released CCK acts as hormone reaching the stomach via the blood-circulation. It mainly causes relaxation of the reservoir. Additionally, it stimulates CCK-receptors on the afferent vagal fibres of the intestinal mucosa and thereby elicits inhibitory entero-gastric reflexes. Thus, via CCK-producing endocrine cells, the intestine is able to recognise luminal nutrients before they are absorbed. Besides CCK, further hormones involved in the feedback-regulation of gastric emptying are the peptide YY and the glucagon-like peptide (GLP-1). These are mainly released from distal small intestine and play a major role in the ileal brake. The feedback-inhibition induced by nutrients mainly depends on the number of receptors stimulated along the intestine. Therefore both the amounts of nutrients entering the gut and the length of the intestine getting into contact with nutrients enhance the inhibition of gastric emptying. The degree of the feedback-inhibition differs among the three nutrients. However, studies indicated that the amount of energy emptied from the stomach per minute is independent from the nutrient composition of the meal. Although the small intestine has no receptors for the energy of the nutrients, the sum of the stimuli obviously reflects the energy contents of the nutrients.
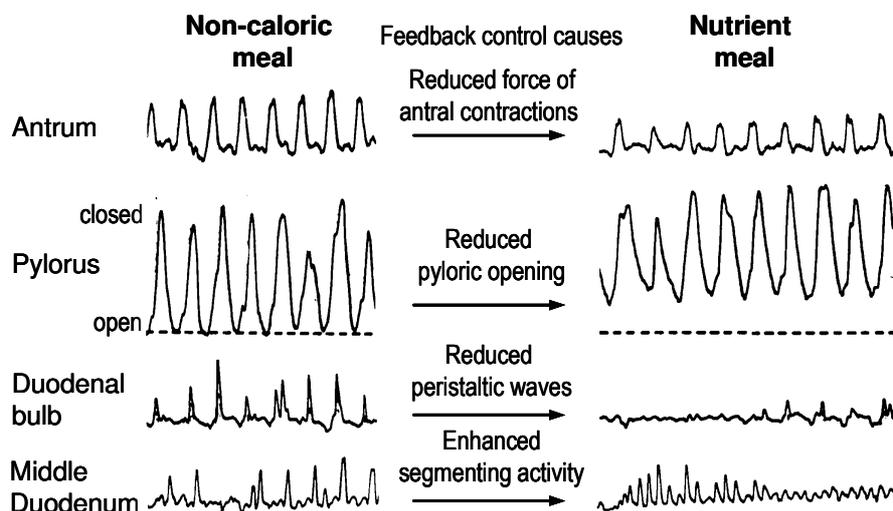

Figure 13 Gastrointestinal motor pattern after a non-caloric and a nutrient meal. Nutrients in the gut activate a feedback control and modulate gastric and duodenal motility.

Figure 14. The feedback-regulation of gastric emptying is performed by entero-gastric reflexes and release of intestinal hormones: an enhanced relaxation of the gastric reservoir is induced by inhibitory vagal fibres (see Fig. 2), an inhibition of the antral pump is caused by a reduced activation of stimulating cholinergic vagal fibres, and a reduced opening of the pyloric sphincter is due to both intestinal hormones and stimulation of cholinergic vagal fibres. Dotted arrows illustrate excitatory enteric pathways releasing ACH or inhibitory enteric pathways releasing NO, VIP PACAP, and/or ATP, respectively.

Studies in pigs on the relationship between gastric emptying and intestinal absorption of nutrients have shown that the absorption of nutrients is characterised by a saturation kinetic which differs among the three nutrients. Carbohydrates are absorbed in larger quantities than protein and fat. However, the amounts of nutrients emptied from the stomach is much lower than the absorption capacity of the intestine. This reduced emptying rate provides a reserve of absorption and enables a constant absorption of energy despite different nutrient composition of the meal. Additionally, after meals which can be easily digested only a part of the intestinal length is required for the complete absorption. This reserve capacity of absorption has obviously the function that all kinds of nutrients – even those with low digestion – are hydrolysed and absorbed before reaching the end of the small intestine. The reserve capacity of absorption is about 2-3 times larger than the amount of nutrients emptied from the stomach. On the other hand, studies have further shown, that an enhanced flow of nutrients into the intestine caused nausea, vomiting and diarrhoea due to an increase in luminal osmolality and influx of water. Thus the reserve capacity of the gut for absorption cannot be used for an increased energy supply. Monogastric animals have an additional reserve capacity for absorption in that only 12 hours are necessary to digest and absorb the daily energy requirement. The remaining 12 hours are used for cleaning the stomach and small intestine. At a short-lasting increase in energy intake the digestive period of the gut is prolonged, while at a long- lasting increase in energy intake the absorption capacity of the gut is enhanced by processes of adaptation.

2   Motility of the small intestine

2.1 Electrical activity

Like in the stomach there is an ICC network located in the intestinal wall between the internal circular and the external longitudinal muscle layers. The ICCs (interstitial cells of Cajal) produce electrical *pacesetter potentials* and initiate slow waves in the smooth muscle cells. The slow waves spread via the gap junctions in aboral direction along the intestine. The frequency of the slow waves and consequently that of the intestinal contractions decreases from the duodenum towards the ileum in a stepwise manner producing frequency plateaus. (Table 1). Along the small intestine, the length of the frequency plateau's decreases, while the resistance in the electrical spread of the slow waves increases. The slow waves of the

small intestine – like in the stomach – determine the maximal frequency of the intestinal contractions (Table 1). Additionally, the length of the frequency plateau's determines the length of the intestinal peristaltic waves, while the resistance in the electrical spread influences the propagation velocity of the peristaltic waves. Thus, the peristaltic waves are far spreading and rapid at the proximal small intestine and become shorter and slower towards the distal gut. This phenomenon contributes to the different transit rates along the intestine. The transport of chyme decreases along the gut in the same proportion as the volume of the luminal contents declines by the absorption of nutrients and water.

2.2   Contractile patterns of the small intestine

In contrast to the stomach, the small intestine produces different contractile patterns (Table 2). Under **physiological** conditions five different contractile patterns occur: **peristaltic waves, stationary segmenting contractions, aboral giant contractions, stationary or migrating clusters of contractions**, and a contractile pattern of the fasting state, called "**phase III**". Furthermore, two **pathological** contractile patterns were found: **giant contractions** moving orally or aborally and **antiperistaltic waves**. Table 2 illustrates in which intestinal segments, in which periods of digestion, and by which stimuli the different contractile patterns occur.

Peristaltic waves are circular constrictions propagating aborally. Due to reflexes initiated by the enteric nervous system they are associated with an aboral relaxation or inhibition of the muscle, respectively. After a non-caloric meal peristaltic waves are the dominant feature (Fig. 15). The peristaltic waves produce an aboral transport of chyme. The propagation velocity of the peristaltic waves is determined by the proximal to distal propagation of the slow waves in the smooth muscle syncitium. In dogs the propagation velocities of the peristaltic waves are: in the duodenum 7-12 cm/s, in the jejunum 4,7 cm/s and in the ileum 0,7-0,8 cm/s (Table. 2).

Stationary contractions occur isolated at single sites without a strict spatiotemporal relation (Fig. 15). They occlude the intestinal lumen pushing the chyme orally and aborally and separating it into segments. Therefore, these contractions are also called "segmenting contractions". The stationary segmenting contractions cause mixing of the luminal contents.
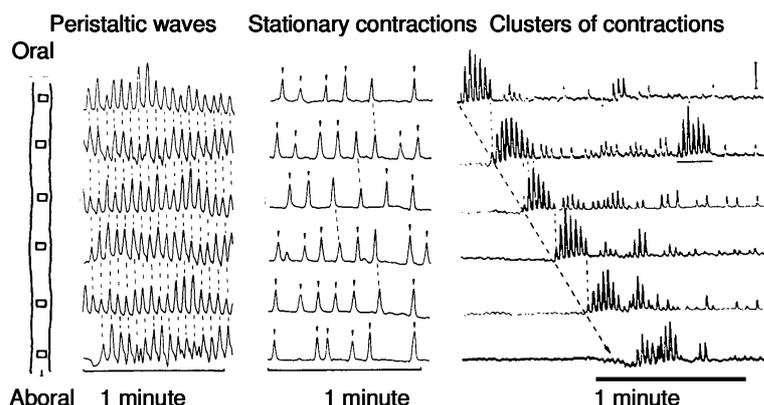

Figure 15. The most frequently occurring contractile patterns of the small intestine are peristaltic waves (indicated by dotted lines), stationary contractions (indicated by arrows), and clusters of contractions, which occur either stationary at an intestinal segment (horizontal line) or slowly migrate aborally (dotted line).

Clusters of contractions and the so called **phase III** represent two complex contractile patterns. Clustered contractions are characterised by several repetitive contractions (Fig. 15). The contractions represent short peristaltic waves pushing the chyme a few centimetres aborally followed by a partial back-flow during the period of relaxation. Thereby the chyme is mixed. When the repetitive short peristaltic waves of the clustered contractions move over the same intestinal segment, the clustered contractions are stationary. In contrast, when each subsequent peristaltic wave starts and ends a few millimetres further aborally, the clustered contractions slowly migrate distally. Clustered contractions usually migrate over a

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short intestinal segment. Both stationary and migrating clusters of contractions frequently occur after a fat meal.

Table 2 Physiological and pathophysiological contractile patterns of the small intestine in dogs

Contractile pattern	Intestinal segment	Occurrence
• Physiological Pattern		
1. Peristaltic waves	total small intestine	non-caloric meal
2. Stationary Contractions	proximal small intestine	Nutrients, espec. protein
3. Aboral giant contractions	distal small intestine	interdigestive (Phase II)
4. Clustered contractions		
a stationary	proximal small intestine	Nutrients, esp. fat
b migrating	total small intestine	Nutrients, esp. fat
5. Phase III	total small intestine	interdigestive
• Pathological pattern		
1. Giant contractions		
a) aborally propagating	proximal small intestine	strong stimuli (acetic acid)
		distal gastrectomy
b) orally propagating	proximal small intestine	Stimuli with vomiting
2. Antiperistaltic waves	proximal small intestine	distal gastrectomy

The **phase III** - also designated as "**migrating motor complex (MMC**) – represents the characteristic motor pattern of the interdigestive period. It consists – like the clusters of contractions – of peristaltic waves which, however, propagate over a longer intestinal segment (Fig. 16). The function of the phase III is described in detail in chapter 3: interdigestive motility.

Jejunal phase III

oral — 1 minute

aboral — Aboral migration of phase III — Velocity of the peristaltic waves
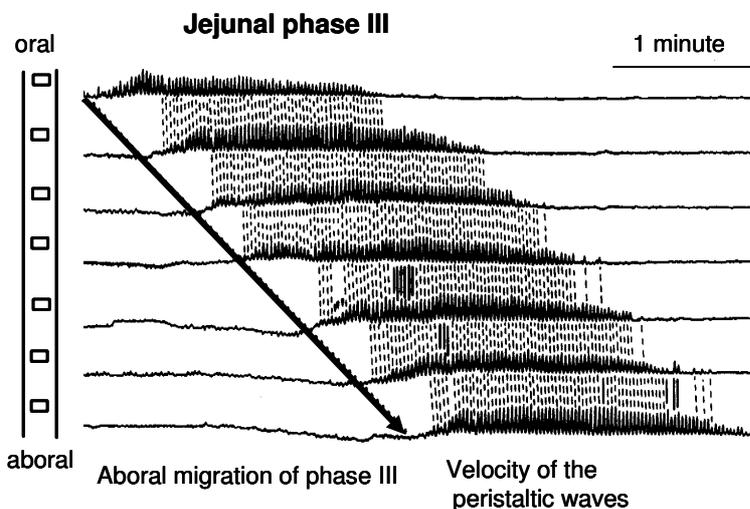
Figure 16. The phase III of the interdigestive motility – also designated as "migrating motor complex" (MMC) – represents a c complex contractile pattern consisting of long peristaltic waves (dotted lines). The phase III slowly migrates aborally (arrow). The aboral migration is caused by each subsequent peristaltic wave starts and ends a few millimetres further aborally.

In comparison with the regular intestinal contractions, the **giant contractions** or **power contractions** are characterised by a large amplitude and a long duration. (Fig. 17). Under physiological conditions they were observed at the ileum during the interdigestive period in dogs, horses and humans. In pigs giant contractions regularly occur at the ileum even during the digestive period. The giant contractions completely occlude the intestinal lumen and propagate slowly in an aboral direction pushing the luminal contents distally and cleaning the intestine. In respect to this procedure they are also called "stripping wave". The propagation velocity of the giant contractions is usually slower than that of the peristaltic waves; in the ileum of dogs it is 0.4 to 0.8 cm/s. Only the postprandial giant contractions of the ileum in pigs have a higher propagation velocity of 3.9 cm/s. In pigs, they produce a regular transport

of chyme from the ileum into the large intestine at intervals of 10-12 minutes. Giant contractions are often the motor *precursor of vomiting*. These giant contractions propagate orally. The occurrence of oral or aboral giant contractions during the postprandial period represents - with exception of the pig - a pathological contractile pattern. Aboral giant contractions of the small intestine are the typical contractile pattern in diarrhoea. In dogs, they can be induced by infections with Cholera toxin or Trichinella spiralis, by radiation, by oral administration of acetic acid or by chemical drugs like Erythromycin, whereas orally propagating giant contractions may be elicited by dopamine or apomorphine.

Antiperistaltic waves of the small intestine are a pathological contractile pattern occurring seldom (Fig. 17). In dogs periods of alternating peristaltic and antiperistaltic waves were frequently observed after distal gastrectomy. The characteristic features of the different intestinal contractile patterns are most clearly recognised by videofluoroscopy.
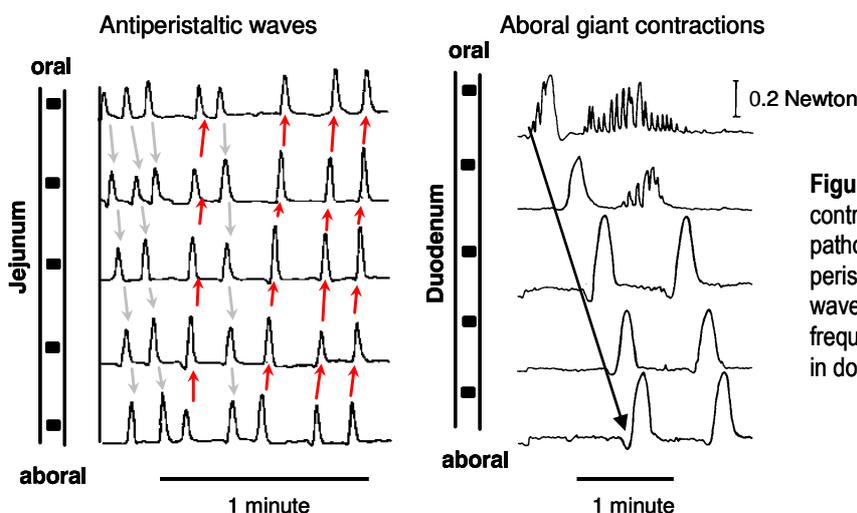
Figure 17. Antiperistaltic waves and giant contractions at the proximal intestine are pathological contractile patterns. Alternating peristaltic (black arrows) and antiperistaltic waves (red arrows) of the jejunum were frequently observed after distal gastrectomy in dogs.

2.3   Origin of contractile patterns

The contractile patterns of the small intestine are caused by the enteric nervous system in connection with the slow waves of the smooth muscle cells. The enteric nervous system produces an inhibitory effect (*neural brake*) on intestinal motility by releasing the inhibitory transmitters NO and VIP. Thereby the slow waves of the smooth muscle cells remain below the spike threshold and the voltage sensitive calcium channels remain closed. Contractions only occur, when the neural brake is released and as a consequence an intestinal segment becomes excitable. This excitation of the intestine by the enteric nervous system can occur independently in space and time and thereby produce different contractile patterns (Table. 3 and Figs. 18 and 19). The peristaltic reflex - the basic circuit of the enteric nervous system – plays an important role. The circuits of the peristaltic reflex are connected with each other by interneurones like a string of pearls. During the excitation of an intestinal segment the circuits of the peristaltic reflex are activated resulting in disinhibition of inhibitory neurones and thus the neural brake is released. Voltage sensitive calcium channels are opened by the release of acetylcholine and the influx of calcium induces action potential discharge as well as the electro-mechanical coupling leading to contractions. In this way the stationary segmenting contractions, the peristaltic waves, the stationary and migrating clusters of contractions and the phase III depend on the slow waves of the smooth muscle cells. In contrast, the giant contractions are independent of the electrical slow waves. They are exclusively controlled by the enteric nervous system: during the occurrence of giant contractions the slow waves of the smooth muscle cells are suppressed and a burst of action potentials slowly moving in oral or aboral direction are produced. It is likely that the enteric nervous system contains hard

wired programs that initiate different contractile patterns and that are triggered by mechanical or chemical stimulation (Fig. 20). There are a variety of additional intermediary cells important to code and transmit the sensory stimulus. The enterochromaffine cell appears to play a key role for transmitting chemical or mechanical stimulation of the mucosa to nerves. In addition it seems crucial that muscle cells maintain a certain tone. Finally, a number of paracrine and endocrine mechanisms are intimately involved in short and long term regulation of contractile patterns. CCK, for instance, stimulates the peristaltic activity whereas in dogs neurotensin mainly produces stationary segmenting contractions. Somatostatin generally has an inhibitory effect on the intestinal motility.
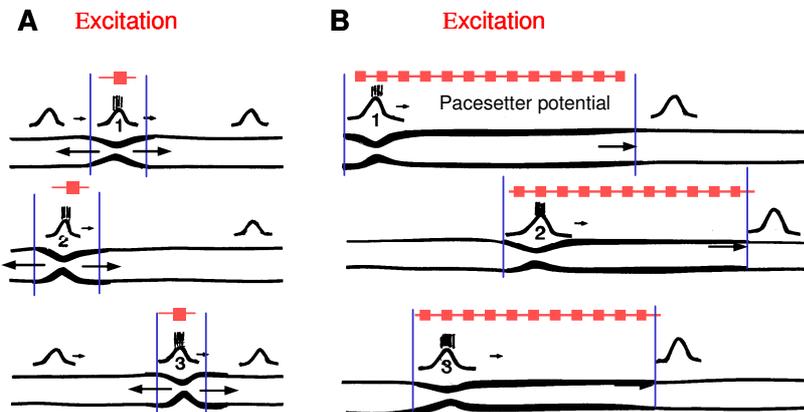
Figure 18. A: Stationary segmenting contractions locally occluding the intestinal lumen are produced by a short excitation of a short intestinal segment. They occur in irregular intervals at various sites of the intestine. They push the chyme both in oral and aboral direction and cause mixing. **B:** Single peristaltic waves are produced by a short excitation of a longer intestinal segment. After meals they occur irregularly at different sites. Red rectangles: excited circuits of the peristaltic reflex. 1, 2, 3, successive pacesetter potentials (slow waves).
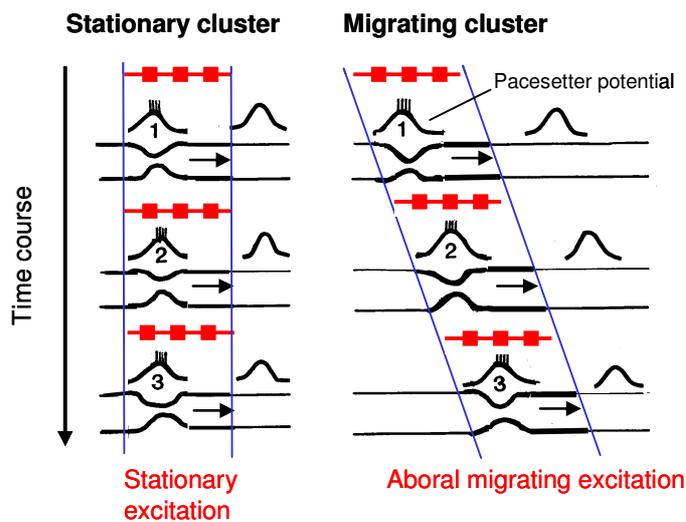
Figure 19. Clustered contractions are produced by a long lasting excitation of a short intestinal segment. The repetitive pacesetter potentials moving along the excited segment cause 4-10 short peristaltic waves at the maximal frequency and thereby a cluster of contractions. The cluster is stationary when the excitation remains at the same segment. When the excitation slowly moves aborally the cluster of contractions migrates along the intestine. The contractile pattern of the migrating motor complex (phase III) corresponds to that of the migrating cluster; however, the excited intestinal segment and thus the length of the peristaltic waves are larger. Red rectangles: excited circuits of the peristaltic reflex. 1, 2, 3 successive pacesetter potentials (slow waves) with spike bursts due to the excitation.
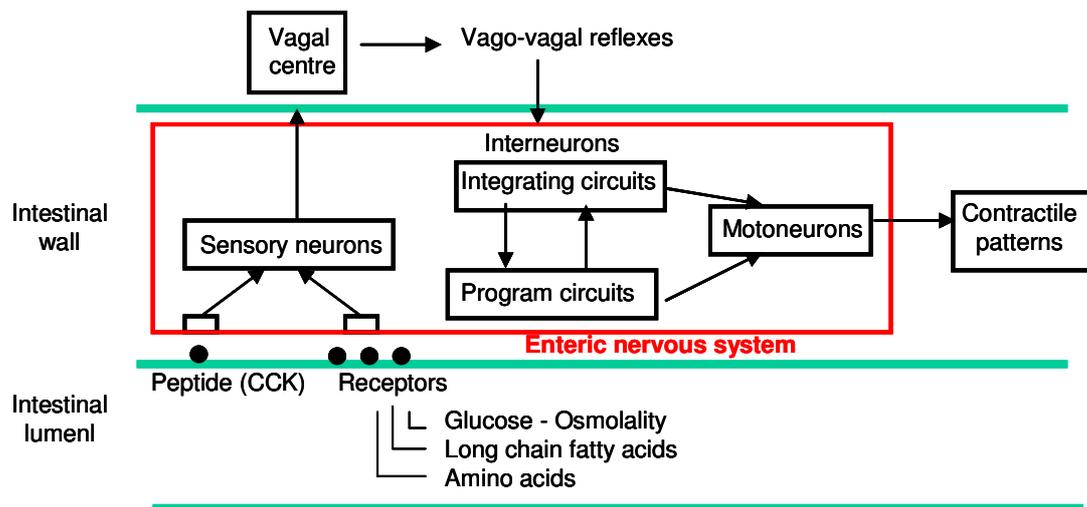
Figure 20. Luminal stimuli elicit vago-vagal reflexes which activate integrating and program circuits of the enteric nervous system. These activate specific motor-neurones responsible for specific contractile pattern.

Table 3. Origin of intestinal contractile patterns by different kinds of excitation.

Contractile pattern	Duration of Excitation	Length of excited segment
Stationary contraction	short	short
Peristaltic waves	short	long
Stationary cluster of contractions	long	short
Migrating cluster of contractions	long	short and migrating aborally
Phase III	long	long and migrating aborally

2.4 Regulation of intestinal motility and of transport of chyme

After a meal the intestinal motility is stimulated by the distension of the gut and is modulated by the luminal nutrients. The **postprandial intestinal motility** is characterised by a mixture of stationary segmenting contractions, clustered contractions and short peristaltic waves (Fig. 21). The segmenting contractions and the stationary clusters of contractions cause mixing of the chyme while single short peristaltic waves and migrating clusters of contractions slowly push the chyme aborally. With increasing filling of distal intestinal segments the motility of the proximal intestine is inhibited. The number of peristaltic waves decreases while the number of stationary segmenting contractions increases. The transport of chyme is mainly determined by the number and the length of the peristaltic waves. This **feedback-regulation**, which is induced by nutrients entering the distal small intestine, does not only reduce gastric emptying but also the flow rate of chyme along the gut. It is the most important control mechanism adapting the flow rate of nutrients to the processes of digestion and absorption.
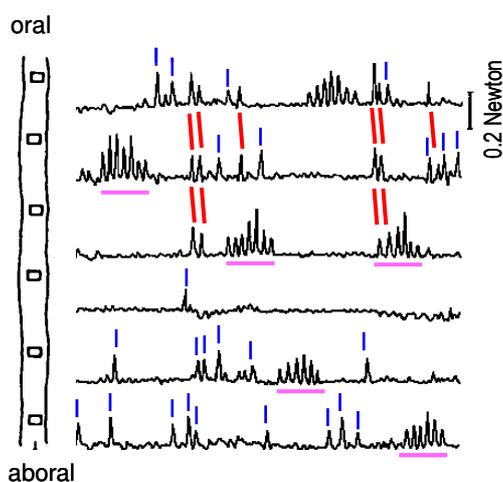
Figure 21. Postprandial contractile patterns of the small intestine are stationary segmenting contractions (blue lines), stationary and migrating clusters of contractions (pink horizontal lines) and single short peristaltic waves (red lines).

3 Interdigestive motility of stomach and small intestine

In omnivores and carnivores the daily energy requirement can be digested and absorbed in about 12 h, therefore, the stomach and small intestine are empty during the remaining period. This interval is designated as **interdigestive period**. However, the empty GI-tract does not persist in a state of motor quiescence, but it produces rhythmically recurring cycles of activity which are called the **interdigestive motility**. In some monogastric herbivores and in ruminants the stomach and small intestine never become empty. Consequently in these animals a clear-cut differentiation between a digestive and an interdigestive period is not possible. Nevertheless, in these animals the characteristic contractile pattern of the interdigestive motility is present.

The interdigestive motility consists of **three phases** designated as phase I, phase II and phase III (Fig. 22). Phase I is a period of motor quiescence, during phase II irregular contractions occur at the small intestine, whereas the **phase III, the migrating motor complex (MMC)**, is characterised by the striking intestinal contractile pattern described above (Figs. 16 and 22).
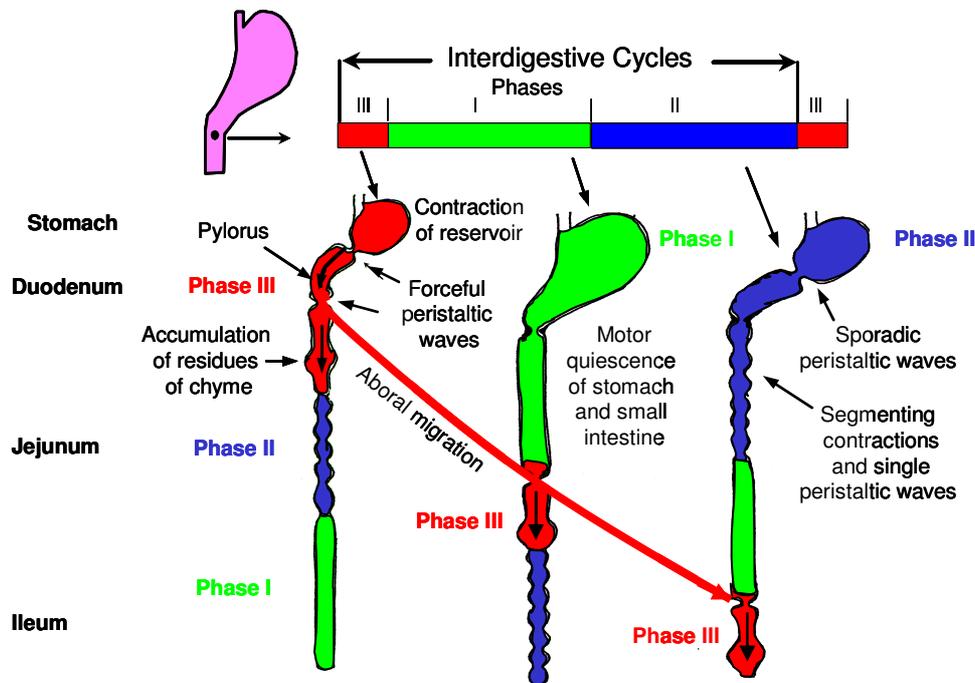
Figure 22. The interdigestive Motility consists of three phases (phase I, II and III). The phase III or the migrating motor complex originates simultaneously at the stomach and duodenum and migrates within 90 to 120 minutes along the small intestine. When a phase III reaches the ileum, the subsequent phase III starts at the stomach and duodenum.

In omnivores and carnivores the three phases cyclically occur. The **duration** of the **interdigestive cycles** differs among species: in dogs and pigs the cycles recur after about 90 min., in rats already after 15 min. The most important motor activity of the interdigestive cycles is the phase III, the MMC. In herbivores the MMC occurs at regular intervals during the digestive period. In sheep, the intervals are about 70 min, in cattle about 80 min and in horses 120 to 150 min. In omnivores and carnivores the phase III originates simultaneously at the stomach and duodenum (Fig. 22). The MMC of the stomach is characterised by 1-3 forceful tonic contractions of the gastric reservoir and lumen occluding peristaltic waves of the antrum occurring at intervals of 2-3 min. (Figs. 22, 23). During the antral contraction the pylorus opens widely and the duodenal bulb relaxes, i.e. there is a pronounced antro-duodenal co-ordination. In contrast to the digestive period, the powerful gastric contractions force residues of chyme and secretions or indigestible particles into the duodenum (Fig. 23).
In this way the stomach is completely cleaned from contents. In dogs, large particles which cannot be ground down by the stomach - like bones, stones of peaches or insoluble tablets – are forced into the intestine by the onset of the interdigestive motility. In herbivores the **gastric phase III** (or migrating motor complex, MMC) is lacking. When a MMC originates at the duodenum, the gastric contractions cease.

In humans and in all animals, with the exception of cats, the migrating motor complex of the small intestine consists of peristaltic waves occurring at the maximal frequency (Fig. 24). They clean the corresponding intestinal segment from residues of chyme and secretions. The duration of the phase III (MMC) at an intestinal segment is in all species about 5 to 7 minutes. The phase III (MMC) slowly migrates from the duodenum along the entire small intestine to the ileum. (Fig. 22). The aboral **migration** of the motor complex - like that of the migrating clusters - is due to a rhythmic spatiotemporal activation and inhibition of intestinal segments resulting in a slow aboral movement of the excited intestinal segment (Fig. 19). The dominant feature of phase III is that successive peristaltic waves start more aboral and propagate slightly beyond the point where the previous one stopped (Fig. 24). Thus the entire motor complex slowly migrates down the intestine, sweeping the lumen clean as it moves along the intestine. The velocity of the aboral migration declines from the proximal to the distal small intestine. It differs among species depending on the intestinal length. In dogs the velocity of migration of the motor complex (phase III) is 6.5 cm/min at the proximal jejunum and 1.7 cm/min at the ileum, while in pigs and sheep the velocity is much faster due

to the greater length of the small intestine: 18 cm/min at the proximal jejunum and 4 or 16 cm/min, respectively, at the ileum. The aboral migration of the motor complex from the duodenum to the ileum lasts 90-120 min in dogs, and 180-190 min in pigs because of the greater intestinal length. In pigs there are 2-3 MMCs simultaneously present at the small intestine, and after a meal the cyclic motor complexes are suppressed only for 1.5–2 h; therefore, in pigs the motor complexes of the intestine recur already during the digestive period like in herbivores and the motor complexes are involved in the postprandial transport of chyme. In cats the interdigestive motor activity consists of giant contractions instead of migrating motor complexes. The main function of the MMC is to clean the small intestine from residues of chyme and secretions. Additionally, the MMC prevents a bacterial overgrowth in the small intestine. The cleaning is supported by an enhanced secretion of gastric and pancreatic juice and of bile occurring immediately before the onset of the MMC.
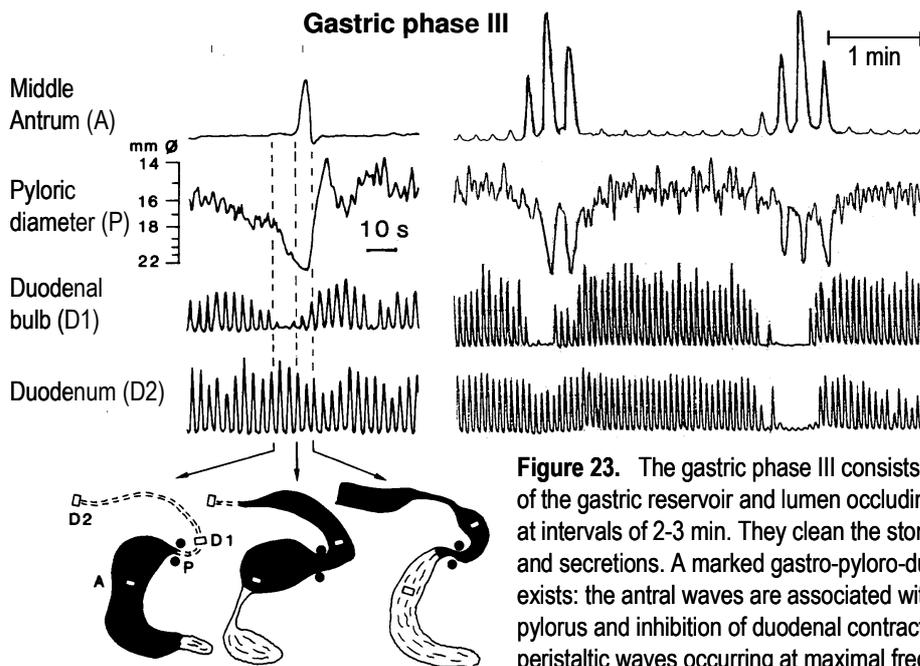
Figure 23. The gastric phase III consists of 1 -3 forceful contractions of the gastric reservoir and lumen occluding peristaltic waves ccurring at intervals of 2-3 min. They clean the stomach of residues of chyme and secretions. A marked gastro-pyloro-duodenal co-ordination exists: the antral waves are associated with a wide opening of the pylorus and inhibition of duodenal contractions followed by duodenal peristaltic waves occurring at maximal frequency.
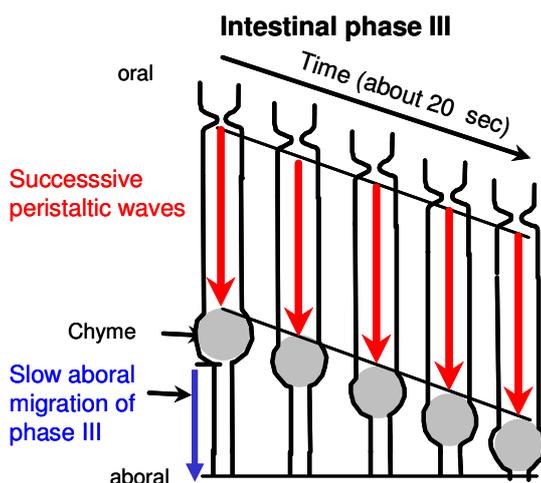

Figure 24. Phase III (MMC) of the small intestine consists of peristaltic waves propagating at maximal frequency along an intestinal segment over a period of 5-10 min. they clean the intestinal segment from chyme which accumulates aborally. Because successive peristaltic waves start and end further aborally the phase III slowly migrates distally.

• Regulation of interdigestive motility

The phase III (MMC) of the interdigestive motility is rhythmically produced by the enteric nervous system. In omnivores and carnivores the origin of the phase III is suppressed by the ingestion of a meal (Fig. 25). Consequently, a postprandial motor pattern occurs. In pigs this inhibition is incomplete. The postprandial suppression of the MMC is caused by neural

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reflexes involving extrinsic nerves (vago-vagal reflexes) as well as by a large number of gastrointestinal hormones. The exogenous administration of various intestinal hormones such as gastrin, secretin or cholecystokinin suppresses the interdigestive motility and the typical postprandial motor pattern recurs. Filling of the GI-tract after a meal also inhibits the phase III via vagal reflexes. When after meals the vagal activity is eliminated by cooling of the vagal nerves the digestive motor pattern ceases and phases III recur. The recurrence of phases III at the end of the postprandial period is facilitated by the release of motilin from endocrine cells of the mucosa. After abdominal surgery the phase III ceases for some hours or days depending on the degree of intervention. The postoperative recurrence of the phase III indicates the restoration of the gastrointestinal functions.
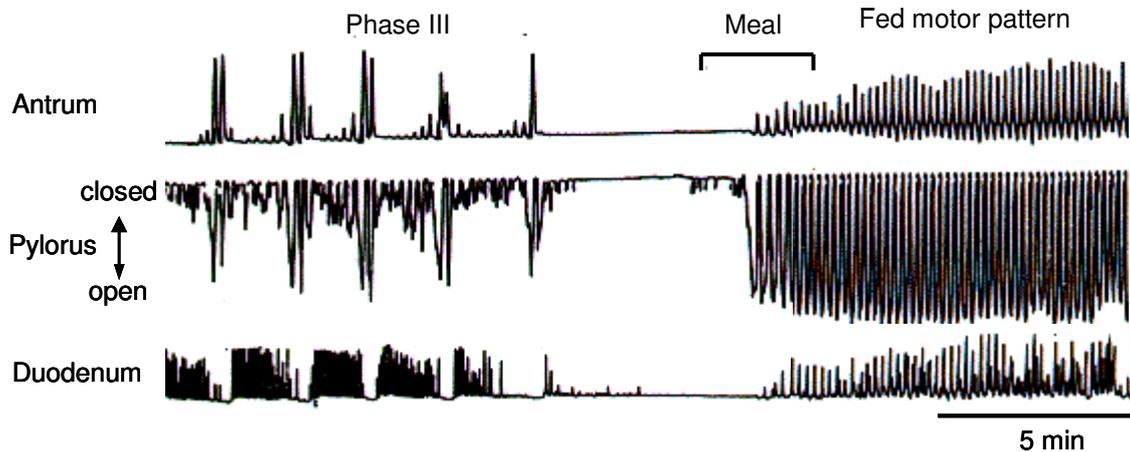

Figure 25. Ingestion of a meal suppresses the interdigestive motility and induces a fed motor pattern. It is characterised by a lower amplitude of the antral waves occurring at maximal frequency, rhythmic pyloric opening and closure and coordinated duodenal contractions occurring in sequence with the antral waves..

4   Motility of large intestine

The large intestine has two main functions: 1) they are fermenting chambers in which fibre and indigestible nutrients are hydrolysed by microbes, and 2) they produce faeces by absorption of water. To fulfil these functions the digesta have to be intensively mixed and slowly moved aborally. Mixing and transport of digesta are caused by 4 different contractile patterns: 1. *peristaltic and antiperistaltic waves,* 2. *aborally migrating segmenting contractions*, 3. *Haustral movements* and 4. *Aborally propagating giant contractions*.

Peristaltic and *antiperistaltic waves* are a characteristic motor pattern of the caecum and proximal colon. As a special feature of the large intestine the circular constrictions of the waves are shallow. Consequently the pro- and retropulsion is low and the flow of digesta across the central opening of the constriction causes an intensive mixing (Fig 26).

The long lasting and aborally *migrating segmenting contractions* represent an unique contractile pattern of the large intestine. They occur most frequently in species producing faecal boli, but they are also a dominant pattern in carnivores. In the literature, the segmenting contractions of the large intestine are designated by different terms. In dogs and horses they are called "colonic motor complex" (CMC). The segmenting contractions separate the digesta into boli (Fig. 26). In contrast to the segmenting contractions of the small intestine which alternately occur at various intestinal sites and last only a few seconds, that of the large intestine represent long lasting circular constrictions occurring simultaneously at adjacent sites and slowly moving distally.
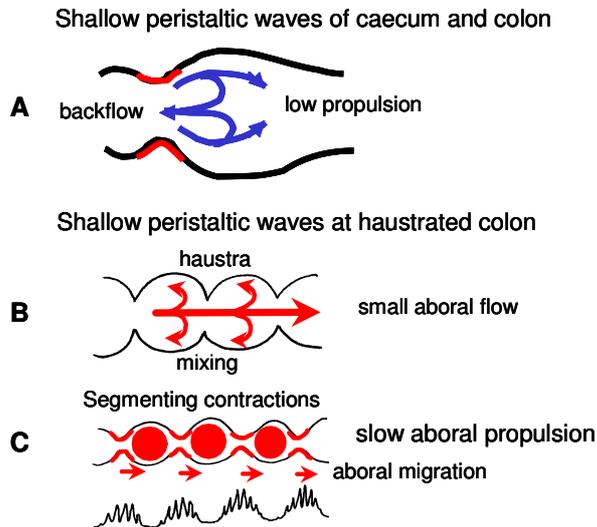
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Shallow peristaltic waves of caecum and colon

A backflow — low propulsion

Shallow peristaltic waves at haustrated colon

B haustra — small aboral flow / mixing

Segmenting contractions

C slow aboral propulsion / aboral migration

Figure 26. A: The peristaltic waves of the caecum and colon produce a shallow circular constriction resulting in a low propulsion associated with back-flow.
B: Peristaltic wave at a haustrated intestine cause a small central flow and mixing of digesta within the haustra.
C: A special feature of the large intestine are multiple segmenting contractions of long duration migrating aborally. Thereby the digesta are divided into boli which are slowly pushed aborally. The motility tracings show a rise of the baseline superimposed by phasic contractions. However, the function of these clusters of contractions differ markedly from that of the small intestine.

   Movements of the haustra of the large intestine are characterised either by alternating contractions and relaxation resulting in mixing of digesta or by an oral or aboral rolling movement causing transport of liquids in a definite direction. Haustral movements are frequently associated with the migrating segmenting contractions. In the motility tracings the segmenting contractions are expressed by an increase in the base-line superimposed by the phasic contractions of the haustra (Fig. 26). This contractile pattern resembles that of the clusters of contractions of the small intestine. However, despite a similar appearance in the motility tracings the clusters of the large intestine represent a completely different motor pattern.

   Aborally propagating **giant contractions** are - like in the small intestine – characterised by their large amplitude, a long duration and a slower propagation velocity compared with the peristaltic waves. They produce a pronounced aboral transport of digesta.

   In the different species the four contractile patterns show some variations in association with morphological differences. Therefore, a detailed description of the motor activity of each species is required. Hitherto, the motility of the large intestine was most intensively investigated in the pig, sheep and rabbit by simultaneous recording of mechanical activity and videofluoroscopy. In the other species the motor function of various segments of the large intestine can only be derived from similarities of motility tracings.

   The frequency and propagation velocity of contraction waves of the large intestine are summarised in Table 4.

Table 4. Frequency and propagation velocity of contraction waves at large intestine in the dog, horse, pig, sheep and rabbit.

Species	Region	Motility pattern	Maximal frequency [contractions/time]	Velocity [cm/second]
Rabbit	Caecum:	Perist.-antiperist. Waves	1 – 2.1/min	1.5
	Colon:	Segmentations	0.46/min	–
		Haustral movements	13.8 – 16.2/min	–
		Giant contractions	0.5/h	1.3 – 3.2
Pig	Colon:	Peristaltic waves	9 – 14/h	2.8 – 5.7
Sheep	Caecum:	Perist.-antiperist. waves	1/min	3.9 – 4.6
		Giant contractions	2 ± 0.3/h	0.6 ± 0.06
	Colon:	Peristaltic waves	12.3 ± 1.8/h	4.7 ± 0.3
		Giant contractions	2.8 ± 0.4/h	0.9 ± 0.4
	Spiral colon:	Peristaltic waves	2.0 ± 0.2/h	2.8 ± 1.5
		Segmentation	2.4/min	7.3 ± 0.6 cm/min
Dog	Colon:	Giant contractions	0.1/h	0.8 ± 0.1
Horse	Colon:	Giant contractions	4.8/h	13.6

4.1   Large intestinal motility of pigs

In pigs the transport of chyme from the ileum into the colon occurs in batches. After a period of stationary segmenting contractions the terminal ileum suddenly relaxes and the chyme is forced into the caecum by a forceful giant contraction (Fig. 27). Such rushes of emptying occur at intervals of 6.5 to 8.5 minutes, i.e. 7 to 9 times per hour depending on the fibre concentration of the meal. In about 70% this flow of chyme is immediately followed by a peristaltic wave of the caecum and colon propelling both the ileal chyme and caecal gas distally along the colon (Fig. 27). Additional peristaltic waves of the colon originate at the beginning of the colonic coil independently from ileal giant contractions (Fig. 27). Thus, peristaltic waves are the dominant motor pattern of the colon in pigs. The frequency of the colonic waves is about 9/h before feeding and increases to 14/h after feeding. The colonic peristaltic waves propagate along the centripetal and centrifugal loops of the colonic coil at velocities of 2.8 and 5.7 cm/s, respectively (Table 4). Each wave propels gas over long distances whereas the colonic digesta are pushed distally only a few centimetres and are simultaneously mixed within the haustra (Fig. 26, B). While the propagation velocity increases, the force of the peristaltic wave declines in distal direction and consequently the transport of digesta slows down. The pronounced haustra of the colon of pigs only show minimal movements and contribute little to a luminal mixing. During the relaxation preceding the colonic peristaltic waves, the haustral constrictions disappear. They are reinforced after the peristaltic wave has passed the colonic segment. When the ileo-caecal flow of digesta is not followed by a peristaltic wave of the caecum and colon (about 30%), the digesta is swept retrograde to the caecal apex by haustral movements of the caecum. The haustral movements of the caecum appear in the motility tracings as clusters of contractions (Fig. 27). The caecum of pigs shows no peristaltic and antiperistaltic waves probably because it is short. In the caecum and first part of the colon a pronounced production of gas occurs due to high rates of fermentation.
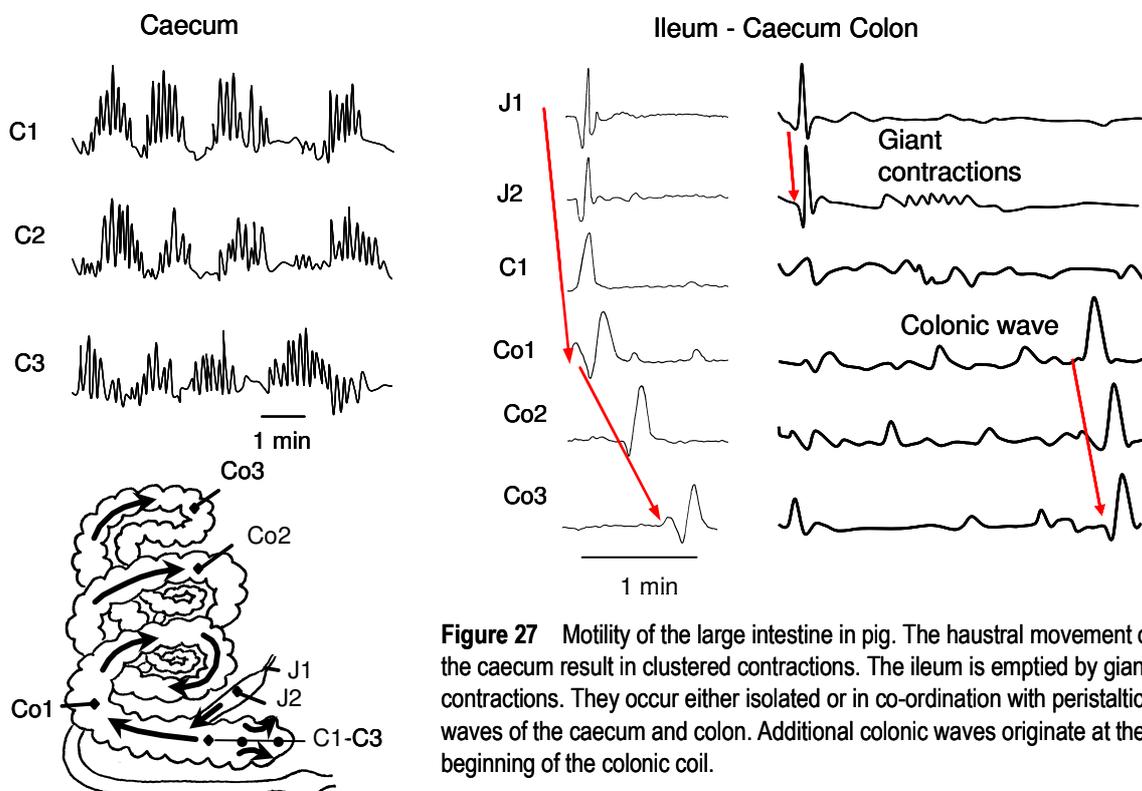

Figure 27   Motility of the large intestine in pig. The haustral movement of the caecum result in clustered contractions. The ileum is emptied by giant contractions. They occur either isolated or in co-ordination with peristaltic waves of the caecum and colon. Additional colonic waves originate at the beginning of the colonic coil.

4.2   Large intestinal motility of sheep

In motility tracings, the aborally migrating segmenting contractions appear as a rise of the base line which, however, is relatively small despite the deep constrictions observed fluoroscopically. This indicates that the segmenting contractions are mainly isotonic contractions, i.e. the shortening of the circular muscle is associated with a low increase in tension. The rise of the base line is superimposed by repetitive phasic contractions so that the motility recordings show clusters of contractions. The mean duration of the clusters is 25s. The phasic contractions represent superficial movements of the intestinal wall mixing the soft chyme of the boli. When a peristaltic wave propagates along the spiral colon, the intestinal segment aboral of the wave relaxes, the segmenting contractions cease for some seconds and the digesta are rapidly propelled distally over various distances, sometimes to the end of the spiral colon.

The transfer of digesta from the ileum into the large intestine occurs both during the migrating motor complex (phase III) and during the remaining period by peristaltic waves often occurring at the maximal frequency of about 15 contractions/min (Table 1). The constrictions of the peristaltic waves are lumen occluding. The ileal peristaltic waves of the sheep show two peculiarities: a very slow propagation velocity of 0.4 cm/s and a long spread over the entire terminal ileum. Due to these features several peristaltic waves are simultaneously present (Fig. 28). They separate the digesta into boli pushing them slowly across the relaxed ileo-caecal sphincter into the caecum.

The motility of the caecum and of the first part of the colon is characterised by peristaltic and antiperistaltic waves. The mean frequency of the peristaltic and antiperistaltic waves is 1/min, the mean propagation velocity is 4.3 cm/s (Table 4). The peristaltic and antiperistaltic waves occur at irregular intervals and propagate over various distances of the caecum (Fig. 28). The contractile force of the waves and consequently the depth of the circular constrictions are also variable. The waves usually do not occlude the lumen and therefore produce a forceful mixing at the caecum and proximal region of the colon (Fig. 26, A). After a period of mixing - around 4.7 min. – the digesta are forced aborally along the colon by peristaltic waves or giant contractions (Fig. 28).
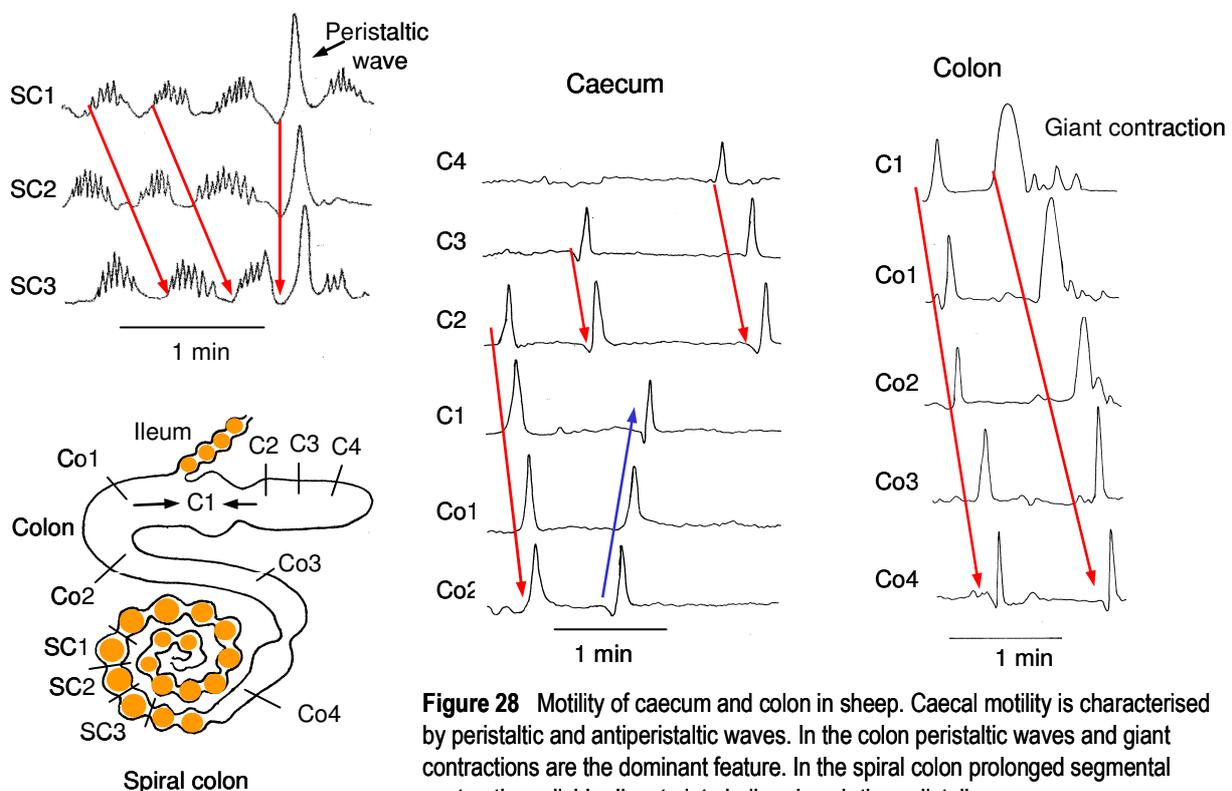

Figure 28 Motility of caecum and colon in sheep. Caecal motility is characterised by peristaltic and antiperistaltic waves. In the colon peristaltic waves and giant contractions are the dominant feature. In the spiral colon prolonged segmental contractions divide digesta into boli and push them distally.

The waves start at the aboral part of the caecum or at the proximal part of the colon. They have a propagation velocity of 4.7 cm/s (Table 4). About 60% of the waves end at region of the proximal colon and about 40% spread to the spiral colon sweeping digesta into the spiral colon (Fig. 28). Some additional peristaltic waves propagate from the middle of the proximal colon to the spiral colon and some further waves originate and end at the spiral colon. The mean frequency of peristaltic waves at the spiral colon is about 2 waves/hour (Table 4). However, the major contractile pattern of the spiral colon consists of long lasting circular constrictions occurring simultaneously at adjacent sites. They divide the digesta into multiple boli. These segmenting contractions slowly move distally at a velocity of 7 cm/min (Table 4 pushing the boli along the spiral colon. (Fig. 28).

A further contractile pattern of the caecum and colon are aboral giant contractions occurring 2 to 2.8 times per hour. They are characterised by large amplitude, long contraction time and low propagation velocity (Fig. 28 and Table 4). They usually propagate over a short intestinal segment. Because the caecum and the proximal colon have a wide lumen, even the giant contractions don't completely occlude the lumen. They produce a larger aboral transport of digesta than the peristaltic waves but don't completely empty the caecum and the proximal colon. The giant contractions are lumen occluding only at the spiral colon resulting in an aboral transfer of the entire luminal content. When the giant contractions or the peristaltic waves of the spiral colon cease the segmenting contractions immediately recur. The mean transit time of digesta along the spiral colon is about one hour. When sheep are grazing the spiral colon shows a higher frequency of peristaltic waves and giant contractions accelerating the transfer of digesta along the spiral colon. Consequently the sheep produce heaps of faeces instead of the small boli.

4.3   Large intestinal motility of cattle

In cattle the motility of the large intestine is similar to that of sheep. However, at the spiral colon peristaltic waves and giant contractions prevail over segmenting contractions. Consequently the transit along the spiral colon is rapid and soft faeces are excreted instead of the faecal boli of sheep.

4.3   Large intestinal motility of rabbits

Rabbits have a relatively large caecum. The caecal motility consists of peristaltic and antiperistaltic waves alternately moving from the caecal base to the apex and from the apex back to the colon (Fig. 29). The frequency of the caecal waves shows diurnal variations with a maximum (2.1 contractions/min) during the night and a minimum (1.0 contractions/min) during the day (Table 4). The peristaltic and antiperistaltic waves predominantly mix the caecal contents (Fig. 29). The flow of digesta from the ileum into the caecum occurs in batches by peristaltic waves. The ileal contractions are usually co-ordinated with caecal antiperistaltic waves so that the ileal digesta are forced towards the apex and mixed with the caecal contents (Fig. 29). The peristaltic waves moving aborally sweep caecal digesta into the proximal colon. The distension of the colon stimulates movements of the 3 rows of haustra: a retrograde rolling movement of the haustra sweeps liquids and suspended substrates from the proximal colon back into the caecum. At the beginning of the single haustrated colon originate – like at the spiral colon of sheep – aborally migrating segmenting contractions Dividing the digesta into boli and pushing them distally. In the tracings the long lasting tonic contractions also appear as rises of the baseline (Fig. 26, C and 29). They are – like in sheep – superimposed by repetitive phasic contractions. Thus the tracings show clusters of contractions. The mean duration of the clusters is 1.5 to 3 min. In rabbits the phasic contractions represent haustral activity. A rolling movement of the haustra sweeps liquids retrograde from the single haustrated to the triple haustrated colon and the caecum while the indigestible solid particles are simultaneously pushed distally by the migrating segmenting contractions. In this way a separation of solids and liquids occurs. The solids are slowly concentrated to the hard faecal boli. In a diurnal rhythm rabbits also excrete soft

faeces. During this period the haustral movements are markedly reduced and the aboral transport of digesta is accelerated by giant contractions (Fig. 29). Consequently, the soft faeces – called *Caecotrophe* - are mainly composed of caecal chyme containing digestible material. The rabbits eat these soft faeces. The production of soft and hard faeces is not only caused by changes in colonic motility but also by modulations of colonic secretion and absorption.
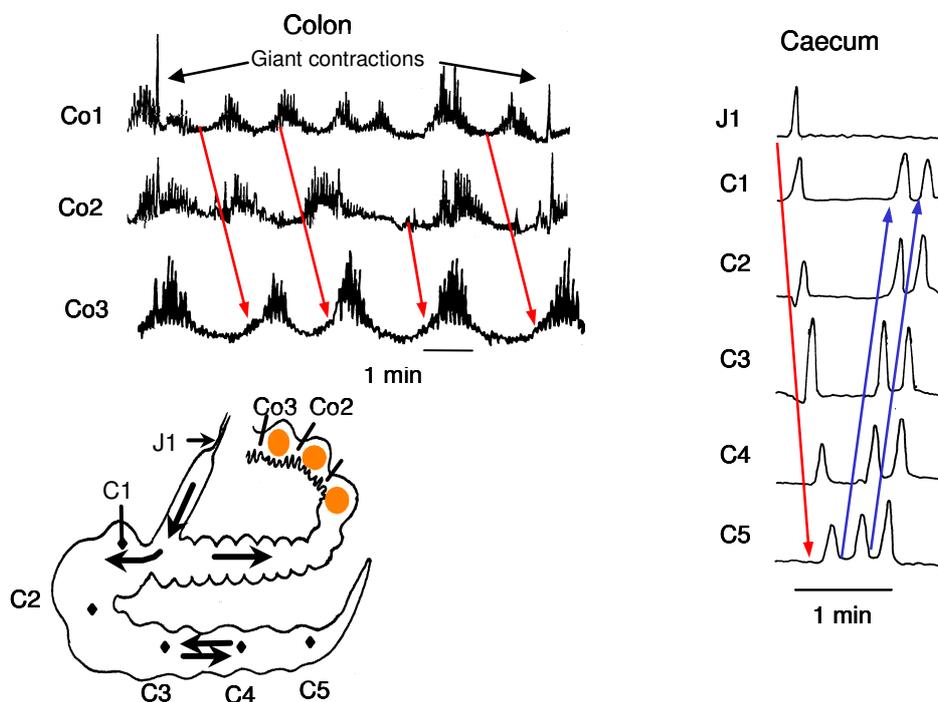

Figure 29 Motor patterns of the large intestine in rabbits. Caecal motility is characterised by peristaltic and antiperistaltic waves. Migrating segmenting contractions are the dominant feature of the single haustrated colon.

4.5 Large intestinal motility of dogs

During the interdigestive period residues of chyme and secretion are transferred from the ileum into the large intestine by migrating clustered contractions, giant contractions and the migrating motor complex (MMC). During the digestive period the flow of chyme into the large intestine occurs irregularly by short peristaltic waves and migrating clusters of contractions.

In dogs the motility of the large intestine was intensively investigated by recording of the electrical or mechanical activity. However, the functions of the contractile patterns remain to be determined. The canine colonic motility consists of organised groups of contractions designated as "*colonic motor complexes*" (CMC's). In the tracings the CMC's have an appearance like the clusters of contractions of the spiral colon of sheep and the single-haustrated colon of rabbits, i.e. they are composed of a rise in base line superimposed by phasic contractions (Fig. 30).
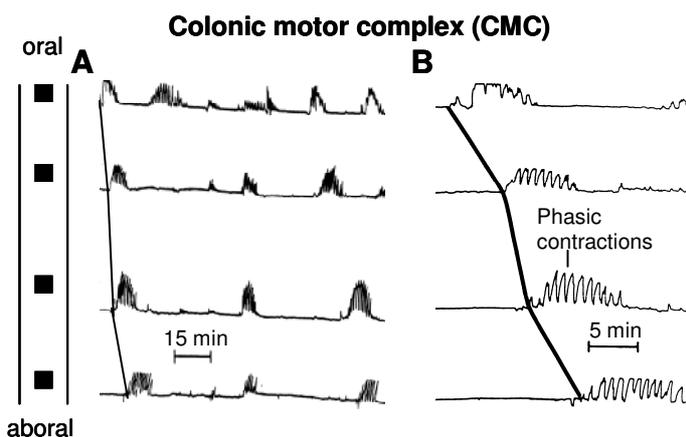

Figure 30. Colonic motor complexes (CMC's) of the canine colon. **A:** Slow paper speed. The CMC's occur at all parts of the colon at intervals of 20-30 min. **B:** High paper speed. The CMC's consist of a rise of the base line superimposed of phasic contractions. The onset of the CMC's obviously differs along the colon (indicated by lines). This was interpreted as an aboral migration of the CMC's. However, such a fast migration within 5-10 min along the entire colon is unlikely. Length of the canine colon is about 45 cm. The intertransducer distances are 12.5 cm.

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In dogs the CMC's don't occur continuously but at intervals of 20 to 30 min followed by a long period of quiescence. The frequency of the CMC's is 1 to 1.6/hour. Due to their isolated occurrence the clustered contractions were designated as "motor complex". The mean duration of the CMC in the proximal and distal colon is 5-9 min and 8-13 min, respectively. In comparison to the clusters of contractions in sheep the prolonged duration of the CMC's in dogs is caused by their larger faecal boli because the cluster lasts so long as the bolus has passed the intestinal recording site by the migrating segmenting contractions (Fig. 26, C). The short periods of activity, the CMC's, occur in the entire colon. As the onset of the CMC's at distal colonic segments is delayed the motility tracings give the misleading impression of an aboral migration of the CMC's. However, the velocity of migration would be extremely high and therefore this relationship is unrealistic. The rise of the base line of the CMC's is probably caused – like in sheep and rabbits - by long lasting, slowly migrating segmenting contractions pushing the faecal boli a few centimetres distally. The function of the superimposed phasic contractions might correspond to that in sheep causing a superficial mixing of the digesta. The long periods of motor quiescence between the canine CMC's might be explained thereby that carnivores ingest small amounts of dietary fibre and consequently only small quantities of digesta have to be transported along the colon.

A second contractile pattern of the canine colon is the *giant contractions*. They occur at intervals of about 10 hours and are often associated with defecation. The giant contraction originates at all segments of the colon and most often propagate to the rectum. Because the deep constrictions of the giant contractions push the entire colonic content aborally they clean large parts of the canine colon.

4.6   Large intestinal motility of horses

The *caecal motility* of horses consists – like in rabbits – of *peristaltic and antiperistaltic waves* occurring rhythmically. Some of the aboral peristaltic waves pass over to the colon pushing caecal digesta into the proximal colon. Besides the peristaltic and antiperistaltic caecal waves a pronounced *haustral activity* with rolling movements was observed.

In horses the motility of the *colon* was only sparsely investigated by fluoroscopy and recording of the electrical activity. Results show some analogies to the colonic motility of dogs, sheep and rabbits. Like in dogs, the colonic motility of horses shows alternated periods of activity and motor quiescence resulting in *colonic motor complexes (CMC*'s).
However, in horses the periods of motor quiescence are short. The CMC's consist – like in dogs - of a rise in the base line superimposed by phasic contractions. The duration of the CMC's is around 3 to 6 min. It is likely that the motor complexes represent aborally migrating segmenting contractions separating the digesta into boli and pushing them distally. The phasic contractions might be haustral movements causing mixing of digesta.

4.7   Gastrocolic reflex

Ingestion of a meal stimulates the motility of the large intestine in dogs and rabbits, while in sheep and pigs the stimulating effect is low. This stimulation is called „**gastrocolic reflex".** Such gastrointestinal reflexes are elicited by distension of the stomach and by nutrients entering the duodenum. Additionally gastrointestinal hormones like CCK and gastrin are also involved in the stimulation of the large intestinal motility. Arrival of digesta at the large intestine causes a further stimulation of motility. This usually occurs 1.5 to 2 hours after the meal. In ruminants and in pigs fed ad libitum the flow of digesta into the large intestine is enhanced when a migrating motor complexes (MMC's) moves over the ileum, afterwards the flow and the motility of the large intestine are diminished for about 10 to 20 minutes.

4.8 Retching and Vomiting

Vomiting is defined as „the forceful expulsion of gastrointestinal contents through the mouth". Vomiting represents a defence reaction to protect the body against the intake of dangerous agents. Toxins in the GI tract can be recognised either before absorption via visceral parasympathetic and sympathetic afferent fibers or after absorption into the blood via the chemoreceptor trigger zone (CTZ) located in the area postrema. The visceral afferent fibers have inputs to the nucleus tractus solitarii – a part of the vomiting center – and parallel inputs to the area postrema. Thus the chemoreceptor trigger zone (CTZ) integrates both the afferent signals from the gastroinestinal tract and the chemical signals from the blood.

Recent studies on gastrointestinal motility have shown that a retrograde giant contraction precedes vomiting (Fig. 31). It originates in the proximal jejunum, propagates orally towards the stomach and moves up to the proximal antrum. The retrograde giant contraction forces the chyme of the proximal small intestine across the widely opened pylorus into the relaxed gastric body. Some minutes later retching and vomiting occurs (Fig. 31). Rhythmic inspiratory movements against a closed glottis produce negative oscillations in intrathoracic pressure and concomitant contractions of the abdominal muscles and the diaphragm cause an increase in intra-abdominal pressure. The distal part of the esophagus containing smooth muscle cells relaxes whereas the proximal striated esophagus contracts resulting in a funnel-like opening of the cardia and the distal esophagus. These rhythmic events during retching cause a repetitive flow of gastric chyme into the esophagus followed by an immediate backflow. Finally, vomiting occurs. In contrast to the events of retching, it is associated with a contraction of the intercostal muscles and an increase in the intrathoracic pressure so that the chyme is forced into the mouth and expelled. Thus during retching and vomiting ejection of gastric contents is not produced by contractions of the stomach but by contractions of skeletal muscles, i.e. by somatic events.
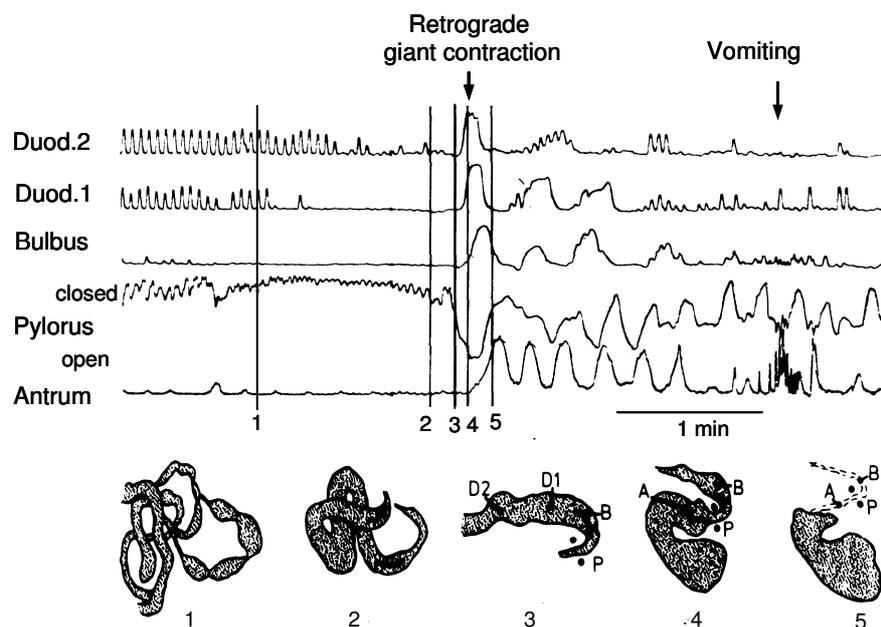

Figure 31. Retrograde giant contraction after apomorphine injection. (1) normal segmenting contractions of the proximal jejunum as seen by radiography; (2) start of a retrograde giant contraction in proximal jejunum; (3) retropelled digesta reach the duodenum and (4) are forced across the widely opened pylorus into the antrum; (5) the giant contraction proceeds to the antrum, the chyme accumulates in the gastric reservoir.