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MECHANISMS OF PROPULSION IN THE SMALL INTESTINE

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Résumé

MECANISMES DE L'ACTIVITE PROPULSIVE DE L'INTESTIN GRELE. — Le débit des ingesta est lié au profil moteur de l'intestin représenté par la récurrence cyclique de complexes myoélectriques (CM) qui présentent, par sommation de 20 en 20 s de la quantité d'électricité des salves de potentiels, 2 phases d'activité rapide : une phase d'activité irrégulière (AI) puis régulière (AR). Les modifications du débit des ingesta au niveau proximal s'accompagnent de variations relatives du nombre, de la durée, de l'origine et de la vitesse de propagation des complexes. La non-propagation des complexes sur la partie distale de l'intestin grêle explique la réduction du débit à ce niveau et la relative autonomie motrice de l'iléon terminal. Au-delà de 48 h de jeûne chez le mouton, l'activité rapide de l'iléon terminal est réduite de plus de 55 % par rapport aux conditions standard. L'activité motrice continue liée à la prise de nourriture chez le rat et le chien d'une part, et l'activité autonome de l'iléon au cours de la suralimentation chez le mouton d'autre part, représentent des modifications extrêmes du profil moteur de base de l'intestin.

Introduction

The interest in improving the utilization of feedstuffs by animals has led to numerous studies on the rate of passage of digesta along the small intestine. Among them, animals surgically fitted with simple or re-entrant cannulas in either the duodenum, jejunum or ileum have been used to measure the flow of digesta. The mean retention times of markers such as polyethylene-glycol (PEG) or $^{51}$Cr-EDTA have also been used to estimate the time available for digestion and absorption of nutrients in different parts of the small intestine. Results in domestic species show that flow of digesta observed in the distal part of the small intestine in sheep is only half of the duodenal flow (Braude et al., 1976); and that of the retention time of digesta is threefold increased in this distal portion (Grovum and Williams, 1973).

In the same order, in rats, Poulakos and Kent (1973) observed considerable differences in rate of propulsion between proximal and distal small intestine.

With the evidence that the velocity of digesta transit is determined by the migration of the myo-electric complex regulating in consequence the rate of flow of small
intestine contents (Bueno et al., 1975; Summers et al., 1976), a new point of interest is how this propagative mechanism regulates the propulsion of contents from jejunum to ileum. In both dogs and sheep the velocity at which the myo-electric complex passes from one site to the other decreases with distance from the pylorus, particularly on the ileum, and a large proportion of migrating complexes (30%) disappears in the lower part of the small intestine (Grivel and Ruckebusch, 1972), a point recently confirmed in dogs (Itoh et al., 1976). In contrast, overfeeding of concentrates in sheep and subsequent increased flow rate of digesta are associated with reduced migration of the myo-electric complex and a reduction in the phases of quiescence (Bueno, 1977). After feeding in dogs, the continuous occurrence of irregular spiking activity at the expense of the phases of quiescence (Bueno et al., 1975) might thus be postulated as an extreme variation of the basic myo-electric complex pattern produced by neurohormonal influences.

As a challenge to the concept of the myo-electric complex as a pattern of motor activity restricted to the interdigestive state (Szurszewski, 1969), the hypothesis already suggested (Ruckebusch and Bueno, 1975) that (i) the myo-electric complex is a basic and intrinsic pattern of activity of the small intestine and (ii) that variations of volume of intestinal contents is associated with specific variations of the characteristics of motor profile, was investigated here.

**Methods**

**Animal preparation.**

Recordings of the electrical activity and measurements of the propagation of the myo-electric complex were obtained from four mongrel dogs, five sheep (Lacaune breed) and ten male Wistar rats. The dogs weighed from 15 to 17 kg, the sheep from 40 to 50 kg and the rats from 200 to 300 g. Animals were housed singly and intestinal electrodes were inserted under anesthesia with thiopental (dogs and sheep) or ether (rats) with aseptic precautions (see Ruckebusch, 1970). Five pairs of electrodes 2 mm apart were implanted as follows:

- dogs: duodenum at 40 cm from the pylorus, middle jejunum at 80, 120 and 160 cm from the pylorus and ileum at 40 cm from the ileo-colonic junction;
- sheep: proximal part of the small intestine at 2 and 7 m from the pylorus, distal part at 17 and 22 m from the pylorus and one pair on the antrum;
- rats: jejunum at 30 cm from the pylorus, four sequential pairs at intervals of 10 cm on the distal part of the small intestine, the last site being located at 20 cm from the ileo-caecal junction.

At the time of surgery a duodenal catheter was inserted in both dog and sheep at 10 cm from the pylorus and a jejunal cannula was placed respectively at 1 and 4 m from the pylorus. Flow of digesta was determined during all the alimentary experimental conditions using a continuous duodenal infusion (3 ml/min) of PEG (Bueno et al., 1975).

**Record analysis.**

Recordings were started 5 to 10 days after operation and prolonged according to the species and subject from 3 weeks to 6 months. The electrical activity was recorded for 1 or 2 hr each day with an EEG machine (Reega VIII, Alvar, Paris) at a time constant of 0.1 sec and continuously plotted at 20-sec intervals during periods of 5 days for 5 sites by a multiple linear integrator circuit (Latour, 1973) connected to a potentiometric recorder (E. and M. Narco, Houston). Each 5-day record was subjected to analysis of the frequency of occurrence, duration, and velocity of propagation of the spiking activity which exhibited cyclically a phase of regular spiking (RSA) in which spike bursts were superimposed on all slow waves. Each regular phase was preceded by a period of irregular spiking activity (ISA) and followed by a quiescent phase.

**Experimental design.**

Dogs received once daily 600 g of canned food (Fido: dry matter 20%, protein 10%, fat 6%, fibre 1%, ash 2.5%) during 3 weeks and 400 g of dried food (Royal Canin: dry matter 60%, protein 32%, fat 18%, fibre 4%, ash 6%) during another period of
3 weeks. Water was offered ad libitum. Comparisons of the electrical spiking activity were made for periods of 24 hr when the complete ration of the canned or dried meal was ingested. The dried meal contained approximately twice the nutrients and digestive bulk present in the canned food.

Sheep received hay ad libitum, the mean intake being 1 200 g/day for 3 weeks. Thereafter, a daily amount of 800 g of concentrates was added to the hay regimen for a further period of 3 weeks during which all subjects reduced their intake of hay by 15 to 20%. Comparisons were made of the activity recorded when the amount of feed available was increased from 1 200 g (hay) to 1 800 g (hay and concentrates).

Rats placed on a 12:12 light-dark schedule received lab chow and water ad libitum and food was withheld, but not water, during one night per week. The animals were accustomed to this routine for a period of two months before the experiments and for all subjects spontaneous feeding occurred during the night-time. Recordings made on the days following normal night-time feeding and overnight fasting were compared.

In each of the three species, recordings made from each subject after a 48-hr period of fasting were considered as representative of the lowest flow rate of digesta.

**Results**

**Level of digestive bulk and its effects on the myoelectric activity in normal feeding conditions.**

**Dog.**

A daily intake of 600 g of canned food with 20% dry matter, was accompanied by changes in the rate of flow of duodenal contents varying from 436 ± 125 ml/hr to 129 ± 17 ml/hr respectively 1 hr and 10 hr after the meal (Table 1). In these conditions, irregular spiking activity was recorded for 8.1 ± 0.8 hr after the meal and the dogs exhibited a basic pattern of 7 to 9 complexes per day with a mean duration of 35 min for the phase of irregular spiking activity and of 7 min for that of regular spiking.

When digestive bulk was increased by a mean daily intake of 400 g of dried food with 60% dry matter diluted in 1 l of water, the number of complexes varied from 5 to 7 per day with a mean duration of 45.2 ± 13.4 min for the phase of irregular spiking activity while that of regular spiking activity was maintained at about 7 min. Continuous irregular spiking activity was recorded for 11.2 ± 1.4 after feeding (Fig. 1). One hour after

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**Table 1:** Comparative relationship between the level of digestive bulk and the intestinal electrical profile in dog and sheep

Canned food was a 600 g meal of a standard canned food with 20% dry matter. Dried food corresponds to a meal of 400 g of dried food containing 60% of dry matter diluted with one litre of water. (a) and (b) : respectively 1 hr and 10 hr after feeding.

<table>
<thead>
<tr>
<th></th>
<th>Flow rate of digesta (ml/hr)</th>
<th>Postprandial disorganization (hr)</th>
<th>Number of MMC/24 hr (Duodenum)</th>
<th>Duration ISA (min)</th>
<th>RSA</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>DOG (n = 4)</strong></td>
<td></td>
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<tr>
<td>Canned food</td>
<td>436 ± 125</td>
<td>129 ± 17</td>
<td>8.1 ± 0.8</td>
<td>9-9</td>
<td>39.9 ± 7.8</td>
</tr>
<tr>
<td>Dried food + water</td>
<td>461 ± 92</td>
<td>174 ± 31</td>
<td>11.2 ± 1.4</td>
<td>5-7</td>
<td>55.2 ± 13.4</td>
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<tr>
<td><strong>SHEEP (n = 3)</strong></td>
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<tr>
<td>Hay</td>
<td>382 ± 87</td>
<td>—</td>
<td>17-19</td>
<td>50.1 ± 15.1</td>
<td>5.4 ± 0.8</td>
</tr>
<tr>
<td>Hay + concentrates</td>
<td>510 ± 121</td>
<td>—</td>
<td>10-15</td>
<td>74.7 ± 22.1</td>
<td>5.6 ± 1.2</td>
</tr>
</tbody>
</table>

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feeding, the duodenal flow rate was not different from that observed for the control canned food meal (461 ± 92 ml/hr) but nine hours later the flow rate was significantly higher (35.2 %) [Table 1].

The velocity of propagation of the complexes on the duodeno-jejunal portions was comparable in the two alimentary conditions from 12 to 18 hr after feeding respectively 3.7 ± 0.8 and 4.0 ± 1.0 cm/min for the low and the high levels of digestive bulk.

An increase in the duration of the irregular spiking activity on the distal part (ileum) associated to a slowing of the transit for about 50% was similar in the two cases.

We noted that in the case of a high digestive bulk (diluted dried food), only one complex was present on the small intestine. In contrast, with the canned food, two complexes were simultaneously present on the duodenum and the terminal part of the ileum.

In the event that a phase of irregular spiking activity was recorded at 40 cm from the pylorus when the previous RSA phase had traversed only 50 to 60% of the intestine length, this new complex faded out before reaching the ileum.

**Sheep.**

On a normal regimen of hay, offered ad libitum, with a mean food intake of about 1200 g per day, the mean duodenal flow of digesta was 392 ± 87 ml/hr. Concomitantly, the intestinal motility exhibited from 17 to 19 complexes per day with a mean duration of 50.1 ± 15.1 min and 5.4 ± 0.8 min for the phases of irregular and regular spiking activity respectively. The complexes were propagated at a mean velocity of 18.9 ± 5.7 cm per min from the duodenum to the ileum, with the highest value on the proximal part of the small intestine. As shown in Fig. 2, only 12 complexes from the 17-19 starting on the duodenum reached the ileum, and supernumerary complexes
Fig. 2: Integrated record of electrical spiking activity during a 48-hr period in sheep on a normal hay diet. Electrodes sites at 2, 7, 17 and 22 metres from the gastroduodenal junction. The incidence of MMCs is 36.8% less in the ileum that in the duodenum.
(2 or 3 per day) started on the jejunum (cf. Fig. 1 from top to bottom respectively at 11:30, 04:00, 16:00, 03:00). For a daily intake of 1 600-1 800 g of mixed hay and concentrates, the duodenal mean flow rate was $510 \pm 121$ ml/hr. The velocity of propagation of the complexes and the duration of the phases of regular spiking activity remained unchanged but their number decreased with values as low as 15 on the duodenum and 10 on the ileum. At the jejunal level, i.e. for electrode sites at 7 and 17 m from the pylorus, from 8 to 12 supernumerary complexes per day were recorded. The duration of the phases of irregular spiking activity was increased to 75 min. No significative change in the pattern was observed during feeding of concentrates.

**Rats.**

In rats, almost continuous irregular spiking activity was recorded during feeding at night-time and the electrical spiking became regularly interspersed with periods of quiescence during the daytime. The corresponding integrated record shows myo-electric complexes recurring at intervals of 60-80 min during 2 to 3 hr (Fig. 3) and then, by reduction in duration of the phases of irregular spiking activity, at intervals of 20 min. When food was withheld during the usual period of feeding, the complexes recurred at intervals of 15 min and the phases of irregular spiking activity lasted only a few minutes on the upper part of the small intestine. In addition, numerous complexes recorded at the jejunal level did not reach the ileum (Fig. 3).

**Effects of fasting on the myo-electric complex and the flow of digesta.**

At the end of a 48-hr fasting period, the flow of digesta was probably reduced in the small intestine in all studied species and this reduction which corresponded to an increase of retention time and a low flow of digesta was always associated in dog, sheep and rat with the continuous migration of the MMC.

**Dogs.**

An increase in duration of the phases of quiescence with a reduction in duration of the electrical spiking activity was the first phenomenon observed 24 hr after a meal and associated with a decrease of 42% in the flow of digesta compared to 10 hours after feeding. This event was paralleled
by a high percentage (50%) of complexes which never reached the ileum, the distal part of the small intestine exhibiting phases of low level irregular spiking activity interspersed with prolonged periods of quiescence. Towards the end of a period of fasting, the complexes were reduced in number and the velocity of propagation for some of them was increased.

Sheep.

The level of antral spiking activity decreased from 24 to 36 hr after food withdrawal and the cyclic inhibition of this activity at the onset of a phase of regular spiking activity was prolonged, particularly after a 48 hr fasting period: 36.1 ± 4.5 min in place of 16.3 ± 3.7 min on hay ad libitum. The mean flow rate was 189 ± 72 ml/hr and the mean duration of each phase of the complex was modified: that of irregular spiking activity was decreased (35.2 ± 7.5 vs. 50.1 ± 15.1 min) and that of regular spiking activity was increased (7.5 ± 0.5 vs. 5.4 ± 0.8 min). The mean number of myoelectric complexes in both duodenum and ileum averaged 15 on the 2nd day of fasting and the mean velocity of propagation was increased from 20 to 34 cm/min although the MMCs recurred at intervals similar to normal food intake (85 min instead of 76 min). The number of complexes recorded at the ileal level was reduced to 4 or 5/day 48 hr after fasting and disappeared 2 days later.

Rats.

After 24 hr fasting subsequent disorders of the motor profile of the small intestine consisted of a reduction in the number of myoelectric complexes at 30 cm from the pylorus from 4 to 1.8 per hour with an increase in duration of the phases of quiescence (12 versus 6 min). Approximately two-thirds of all phases observed disappeared before the last 50 cm of the small intestine. Towards the end of the period of fasting the level of irregular spiking activity became very low and that of regular spiking activity was less well-defined. At this time, feeding enhanced irregular spiking activity which replaced both the quiescence and the phase of regular spiking activity.

Discussion

A cyclic, recurring, migrating myo-electric complex (MMC) of the small intestine was firstly described by Szurszewski (1969) in fasted dogs and was therefore regarded as interdigestive by Carlson et al. (1972). The strongest contractions, i.e. the activity front (Code and Mariett, 1975) or the phase of regular spiking activity (Bueno et al., 1975; Ruckebusch and Fioramonti, 1975), occur in an empty gastrointestinal tract is a paradoxical finding. A challenge to the concept of the MMC as a «housekeeper» of the small bowel observed in the interdigestive state, was given by Grivel and Ruckebusch (1972). In a comparative study in dogs, rabbits and sheep, they found that the MMCs were permanently present regardless of feeding in rabbits and sheep and that, for both dogs and sheep, about 30% of the MMCs starting at the duodenal level did not migrate caudally but simply disappeared after traversing 60% (dogs) and 40% (sheep) of the length of the small intestine when the flow of digesta was decreased. This view of the myoelectric complex as a basic pattern of the small intestine which was disrupted to varying extents by feeding, according to the species, was extended by a study of the motor profile of the gut in pigs. When fed ad libitum, the motility pattern resembles that seen in ruminants where the myoelectric complex persists regardless of feeding (Ruckebusch and Bueno, 1975). Code and Mariett (1975) found that only 3 of 67 complexes observed in 5 dogs during 6-hr recording sessions failed to reach the ileum. These authors discussed the possibility that unusual manipulations of animals might be the origin of the high incidence of disappearance of migrating activity.

Discussion

A cyclic, recurring, migrating myo-electric complex (MMC) of the small intestine was firstly described by Szurszewski (1969) in fasted dogs and was therefore regarded as interdigestive by Carlson et al. (1972). That the strongest contractions, i.e. the activity front (Code and Mariett, 1975) or the phase of regular spiking activity (Bueno et al., 1975; Ruckebusch and Fioramonti, 1975), occur in an empty gastrointestinal tract is a paradoxical finding. A challenge to the concept of the MMC as a «housekeeper» of the small bowel observed in the interdigestive state, was given by Grivel and Ruckebusch (1972). In a comparative study in dogs, rabbits and sheep, they found that the MMCs were permanently present regardless of feeding in rabbits and sheep and that, for both dogs and sheep, about 30% of the MMCs starting at the duodenal level did not migrate caudally but simply disappeared after traversing 60% (dogs) and 40% (sheep) of the length of the small intestine when the flow of digesta was decreased. This view of the myoelectric complex as a basic pattern of the small intestine which was disrupted to varying extents by feeding, according to the species, was extended by a study of the motor profile of the gut in pigs. When fed ad libitum, the motility pattern resembles that seen in ruminants where the myoelectric complex persists regardless of feeding (Ruckebusch and Bueno, 1975). Code and Mariett (1975) found that only 3 of 67 complexes observed in 5 dogs during 6-hr recording sessions failed to reach the ileum. These authors discussed the possibility that unusual manipulations of animals might be the origin of the high incidence of disappearance of migrating activity.

With the use of integration of spike bursts at 20-sec intervals, it became relatively easy to follow the alternation of quiescent and spiking phases of the small intestine for periods as long as 3 months. In all species studied to date, i.e. rat, rabbit, dog, sheep, cow and horse, a number of complexes faded out in the lower part of the small intestine. In dog, no more than one complex at a time can exist in the proximal 70% of the gastrointestinal tract and, according to Itoh et al., (1976), if a new complex starts before the previous has traversed
70% of the small intestine, this new complex disappears. Present results indicate that about 30% of the myo-electric complexes recorded at the jejunal level fail to reach the ileum and that this phenomenon is enhanced by fasting.

The concept that propulsive activity of the small intestine is directly mediated by the myo-electric complex is refined by the assumption that the phase of irregular spiking activity is directly related to the volume of food residues and chyme, and that the subsequent regular spiking phase acts as an aboral barrier (Bueno et al., 1975). In this previous work, we have shown that in sheep under normal regimen, the time of transit was related to the velocity of MMC's propagation and that in this species like in dogs, an experimental increase of 40-45% of the flow rate of digesta disrupted the MMC pattern. The present experiments have demonstrated that physiological increase of the flow rate of digesta induced changes but not disruption of the MMC pattern.

We suggested that the adaptation of the intestine to a moderate increase of the flow rate was more dependent of the intestinal volume than of the motor factors (except for the duration of ISA); in contrast, the motility pattern changed in relation to a consequent increase (40%) of the flow rate of digesta. The fact that a capsule can move from the stomach to the proximal ileum in 20-40 min but requires a further two hours to pass the distal ileum is emphasized by the fading out of the regular spiking phase of a myo-electric complex after traversing 60% of the small intestine. After feeding, the propulsion of the increased volume of digesta involves continuous irregular spiking activity without quiescence, the gradient of pressure usually linked to the development of the phase of regular spiking activity being unnecessary for a continuous flow of gastric contents. On the other hand, a few hours after feeding, when gastric emptying is moderate, phases of quiescence preceded by phases of regular spiking activity provide the characteristic intermittent flow of digestive contents (Bueno et al., 1975). Particularly worthy of mention is that, when the volume of digestive contents is reduced, for example in sheep, the myoelectric complexes recur at increased intervals and their phase of regular spiking activity is increased in duration (Bueno, 1977). When no other propulsion than that of desquamated cells and secretions of the small intestine is involved, it is characterized by a low level of irregular spiking activity with phases of regular spiking activity.

( Accepted for publication, June 1977.)

Summary

In sheep like in rats 2 hr after feeding and in fasting dogs, the rate of passage of digesta along the small intestine is related to the migration of the myo-electric complexes (MMCs). The modifications of this basic common pattern and that of its two consecutive irregular and regular phases were related to changes in the flow of digesta in both the proximal and distal parts of the small intestine. A high flow rate in the jejunum is associated to an increase in duration of the phases of ISA and by supernumerary MMCs at this level. Normally at the ileal level, the flow of digesta was lower than in upper parts with an increase in retention time associated both with a slow migration of the complexes and the disappearance of about one third of them after traversing 60% of the length of the small bowel. These experiments suggest that the origin, propagation and frequency of the basic MMC pattern as well as the ratio of ISA to quiescence are operative factors involved in small intestine propulsive activity. The continuous spiking activity seen immediately after feeding in rats and dogs and the autonomous pattern of activity of the ileum during prolonged fasting in sheep represent extreme changes of the basic MMC pattern.
References


