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Ovine small bowel “minute rhythm” intensity related to feeding and phase of migrating myoelectric complex

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ABSTRACT. The presented study was performed to characterize further the ‘minute rhythm’ in the ovine small bowel, notably to assess the role of fasting and feeding as well as of the phase of the MMC upon the number and amplitude of the MR-containing spike bursts. In eight rams the electrodes were attached to the pyloric antrum, duodenal bulb, duodenum and upper jejunum. In the course of chronic experiments, the myoelectrical recordings were conducted in fasted and non-fasted rams, before and after feeding offered during phase 2a or 2b of the MMC. The phases of the MMC and the MR episodes were identified and the MR frequency, the number of the spike bursts in one MR episode and their amplitudes were calculated. 74 per cent of the MR episodes exhibited the propagated character. At the beginning of phase 2a, the MR often arrived exclusively in the duodenal bulb and was disorganized, while at the end of phase 2b of the MMC, the MR-related spike bursts were most prominent and propulsive. In the duodenal bulb, the giant-like spike bursts forming the pattern were observed occasionally. The MR episodes contained usually 1-2 spike bursts. The number of the MR episodes, each containing one spike burst was smaller after feeding mostly in the duodenum and jejunum and it was lower during phase 2b than during phase 2a of the MMC in the duodenal bulb, duodenum and jejunum. The number of the spike bursts in one MR episode increased after feeding and during phase 2b of the migrating myoelectric complex and it was the highest in the jejunum. The spike burst amplitudes of the MR episodes were the highest in the duodenal bulb. Feeding during phase 2b of the MMC decreased the amplitude of the MR-related spike bursts both in the duodenum and the jejunum. It is concluded that the intensity of the MR in the ovine small bowel is related to feeding and to the phase of the MMC and the high variability of the pattern comprises its character and strength that are apparently related to the intraluminal influences affecting the controlling mechanisms.

Key words: ram, duodenum, jejunum, electromyography, motility patterns

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INTRODUCTION

The term 'minute rhythm' (MR) can be defined as repeatable spike bursts or contractions arriving every 1-2 min. It represents the motility pattern also described under the other names used probably because of its high variability. The MR is the classical term of the pattern. It is also named 'clusters of waves' or 'clusters of contractions' or 'repetitive clusters of the spike bursts' (Heddle et al., 1993; Staumont et al., 1992). The event is considered as the regular motility pattern (Husebye, 1999; Sarna and Otterson, 1989). In the ruminant and non-ruminant species it occurs mostly in the small bowel, including the ileum, but it was also identified in the pyloric antrum (Bueno and Fioramonti, 1980; Fleckenstein et al., 1982; Kruis et al., 1985). Existence of the pattern is well established (Bueno and Fioramonti, 1980; Husebye, 1999; Sarna and Otterson, 1989). However, some authors found similar motor events using no specific terminology, i.e. not treating these events as the regular motility patterns (Bueno and Ruckebusch, 1979; Bühner and Ehrlein, 1989; White et al., 1983). Therefore, some doubts still exist regarding the evident identification of the MR resulting from the lack of its precise definition and characterisation. In sheep, its occurrence in the gastrointestinal regions, incidence, relations to the migrating motor complex (MMC) and feeding conditions were described in part, along with its basic features (Bueno and Ruckebusch, 1979; Fleckenstein et al., 1982; Romański, 2002; Romański 2003; Romański, 2007a; Romański, 2009a). However, from its incomplete characteristics neither has been possible to define the pattern more precisely nor to conclude as to the physiological role of the pattern in the digestive system. Thus, the aim of this study was to provide in rams the careful pattern elaboration considering the frequency, propagation, the number of the spike bursts in one MR episode and the amplitude of the spike bursts forming the pattern. Furthermore, the effect of fasting, feeding and the MMC phase upon the intensity of the MR in the duodenal bulb, duodenum and upper jejunum was assessed.

MATERIALS AND METHODS

Eight healthy rams of Polish Merino breed, each weighing 38-44 kg, were used. In all the animals, clinical examinations were performed. Before the experiments, the rams were kept in the natural light-dark cycle and fed with good quality hay and the grain mix-

ture, according to feeding norms for sheep with free access to the drinking water.

Animal preparation

Rams were surgically prepared for the experiments. After general and local anesthesia, the mid-right laparotomy was performed and the distances between the points for electrode localization were measured. Three basic bulbar, duodenal and proximal jejunal platinum bipolar electrodes (located 6, 50 and 250 cm from the pyloric ring, respectively) and two additional electrodes located in the abomasal antrum (4 cm before the pyloric ring) and in the more distal jejunum (300 cm below the pyloric ring) were implanted. The additional electrodes were used to validate further the experimental model by controlling the correctness of the myoelectrical activity recorded throughout all the experiments. At least ten postoperative days were allowed for recovery. Some other details of this experimental procedure were described earlier (Romański, 2002; Romański, 2003; Romański, 2009a).

Experimental design

In the course of the chronic experiments, the myoelectrical activity was recorded in all the animals studied by means of the multichannel electroencephalograph (Reega Duplex TR XVI, Alvar Electronic, Montreuil, Paris). Experiments were performed in 48-h fasted rams (not fed during the experiment), in 48-h fasted rams (fed during the experiment), in non-fasted rams (not fed during the experiments), and in non-fasted rams (fed during the experiment). Feeding procedure (250 g of the grain mixture consumed during 2-3.5 min) was started about 2 min after the onset of phase 2a or 2b of the migrating myoelectric complex (MMC), identified during recording sessions. In all the groups, following the initial recording period, one full MMC cycle was recorded. The total of 48 experiments, each lasting 3-4 h was conducted.

Analysis and interpretation of the electromyographical recordings

The myoelectrical recordings were analysed and the MMC was first identified. The phase 2 of the MMC was subdivided into the (sub)phases 2a and 2b (Dent et al., 1983; Romański, 2002). The small-intestinal MMC was identified as the composed, long-lasting myoelectric activity pattern containing three or four phases (Code and Schlegel, 1973; Szurszewski and

Code, 1968). In sheep, the pattern is similar to those in monogastrics, but absent in the stomach (Grivel, 1971). The 'minute rhythm' (MR) episodes, were identified during phase 2 of the MMC. The MR pattern was considered as the repeatable spike burst(s) of the migrating or non-migrating event occurring mostly in the small bowel (Fleckenstein et al., 1982; Romański, 2002). The character of the MR episodes was visually analysed upon the tracings during the designed observation periods. Ten terminal MR episodes that arrived during phase 2a of the MMC and ten terminal MR episodes during phase 2b of the MMC were analyzed in the given small intestinal region upon the tracings obtained from all the experiments without feeding in order to identify the MR types with one (type 1), two (type 2), three (type 3) or four or more (Type 4) spike bursts in one MR pattern. The same analysis for the ten first MR episode series observed in all the groups of the experiments with feeding, starting just after termination of feeding, was performed. In each group of the experiments and observation periods, the first and last MR episode of each MR series analysed, the amplitude the most prominent spike within the MR-spike burst was measured and used for statistical calculations. However, in the duodenal bulb, the first fully developed MR episode was analysed since usually the first MR pattern arriving during the phase 2a of the MMC was not observed in the lower recording chan-

nel. If the given MR contained more than one spike burst, the greatest spike burst was selected for amplitude measurement.

Statistical analysis

All the data were grouped in tables and the mean values from all the animals studied and all the experiments performed along with standard deviations were calculated. Statistical significances were depicted using the Student t-test for paired values preceded by analysis of variance (Snedecor and Cochran, 1971).

Ethical aspects

The experiments were approved by the II Local Ethical Committee for the Experimental Animals and were performed according to the European laws.

RESULTS

Duration of the MMC cycles, observed during the experiments, ranged from 65-73 min in fasted rams, 81-112 min in non-fasted rams and 79-127 min in the all the groups with feeding. The MR cycles arrived regularly during limited periods either during phase 2a or 2b of the MMC in most of the experiments. Among 640 MR patterns analysed, 473 were propagated, 160 were non-propagated or not well organized (Fig. 1) and 7 were retropropagated. At the beginning

Figure 1. The 'minute rhythm' in small bowel of fasted ram. The mid fragment of phase 2b of the migrating myoelectric complex is presented. Note the relatively low intensity of the myoelectric activity and the short-lasting spike bursts of the pattern. No 'minute rhythm' in abomasal antrum can be identified. At least three episodes of the pattern, not well organized, can be distinguished. The occurrence of the pattern in the lowest channel is doubtful.

Explanations: T – time in seconds; C – electrode calibration, 100 μ V; A - abomasal antrum; B - duodenal bulb; D - duodenum; PJ - proximal jejunum; DJ - more distal jejunum.

Other explanations as in the chapter Material and Methods.



Table 1. The numbers of the spike bursts of the 'minute rhythm (MR) episodes (MR types 1-4) in the duodenal bulb, the duodenum and the jejunum of fasted rams observed during phase 2a or 2b of the migrating myoelectric complex (MMC) in various feeding conditions.

			No feeding				Feeding			
Groups:			1	2	3	4	1	2	3	4
DB	Ph. 2a	Mean	9.8	0.3	0.0	0.0	5.1 ^c	1.8 ^a	1.8 ^c	1.3 ^c
		±S.D.	0.5	0.5	0.0	0.0	1.4	0.9	1.3	1.0
	Ph. 2b	Mean	8.8	0.6	0.5	0.1	6.8	1.1	1.3 ^a	0.9
		±S.D.	1.0	0.9	0.5	0.4	1.7	1.0	1.0	0.6
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D	Ph. 2a	Mean	7.5	1.6	0.6	0.3	2.6 ^c	2.9	2.6 ^a	1.9
		±S.D.	1.9	1.2	0.5	0.5	1.5	0.8	1.5	1.4
	Ph. 2b	Mean	4.0 ^x	3.6 ^x	1.5	0.9	1.9 ^a	2.8	2.9	2.8 ^a
		±S.D.	1.3	1.1	0.9	0.8	1.0	1.3	1.5	0.7
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J	Ph. 2a	Mean	5.0	1.6	2.5	0.9	3.4 ^a	2.3	2.6	1.8
		±S.D.	0.8	0.9	0.5	0.8	1.1	1.4	0.9	1.0
	Ph. 2b	Mean	1.6 ^z	3.1	2.9	2.4	1.4 ^x	1.4	2.6	4.6 ^{cz}
		±S.D.	1.2	1.0	1.0	0.9	1.2	1.2	1.1	0.9

The numbers illustrate the incidence of each of the four types of MR. Ten consecutive MR episodes were identified during phase 2a and 2b of the MMC in the given small intestinal region and classified into the types during the experiments without feeding and during experiments with feeding.

Explanations: Groups 1-4 – MR types. Ph. 2a – phase 2a of the migrating myoelectric complex (MMC). Ph. 2b – phase 2b of the MMC. DB – duodenal bulb. D – duodenum. J – jejunum. Means±S.D., n=8. Statistical significances: ^ap<0.05, ^cp<0.001 vs. relevant value obtained from the experiments without feeding; ^xp<0.05, ^zp<0.001 vs. relevant value obtained during phase 2a of the MMC.

Other explanations as in the section Material and Methods

of phase 2a of the MMC, the MR usually arrived only in the duodenal bulb and it was often disorganized (Fig. 1). Soon after its organization was improved. At the end of phase 2b, the MR-related spike bursts were most prominent and propagated (Fig. 2). In the duodenal bulb, at least 12 giant-like spike bursts forming the MR were observed. Both phasic and tonic components of the MR were recorded in some cases.

In the duodenal bulb of fasted rams, the number of the MR types 2, 3 and 4, observed during phase 2a of the MMC, was significantly greater in the experiments with feeding than in the experiments without feeding (Table 1). These changes occurred at the expense of the number of the MR type 1 that was sig-

nificantly lower in the experiments with feeding as compared with the experiments in which no feeding procedure was applied. When the relevant values, obtained during phase 2b of the MMC, also recorded in the duodenal bulb, were considered, the number of the MR type 3 was significantly higher after feeding than before (Table 1). In the duodenum of fasted rams, the number of the MR type 3 during phase 2a and the number of the MR type 4 during phase 2b of the MMC was greater during feeding than without feeding at the expense of the number of the MR type 1. It was lower in the experiments with feeding than in those without feeding both during phase 2a and 2b of the MMC (Table 1). In the jejunum, the number of the MR type 1 was also significantly lower after feeding than in

the experiments without feeding, and this change occurred mostly at the expense of the increased number of the MR type 4. The number of the MR observed in the fasted rams in the course of phase 2b exhibited often the decreasing tendency as compared with phase 2a of the MMC, both in fed and not fed animals. Especially, significant alterations were denoted in the duodenum in the experiments without feeding, during which the number of the MR type 1 was significantly lower during phase 2b than during phase 2a while the number of the MR type 2 was significantly higher during phase 2b than during phase 2a of the MMC (Table 1). In the jejunum of not fed and fed animals, the number of the MR type 1 was also significantly decreased during phase 2b as compared with phase 2a of the MMC. These changes occurred mostly at the expense of increased number of the MR type 4, espe-

cially in the experiments with feeding (Table 1).

In the duodenal bulb of non-fasted rams, the number of the MR type 4 was slightly but significantly increased during phase 2b of the MMC in the experiments engaging the feeding procedure (Table 2). In the duodenum, in the course of phase 2a of the MMC, the numbers of the MR type 2 and 3 were significantly increased after feeding as compared with the results of the experiments without this procedure. These results occurred at the expense of the MR type 1. Its incidence was significantly decreased after feeding as compared with the results obtained from the experiments with no-feeding procedure (Table 2). In the jejunum, during phase 2a of the MMC, the number of the MR type 1 was significantly reduced after feeding at the expense of slightly enhanced values of the MR type 2,

Table 2. The numbers of the spike bursts of the 'minute rhythm' (MR) episodes (MR types 1-4) in the duodenal bulb, the duodenum and the jejunum of non-fasted rams observed during phase 2a or 2b of the migrating myoelectric complex (MMC) in various feeding conditions.

			No feeding				Feeding			
Groups:			1	2	3	4	1	2	3	4
DB	Ph. 2a	Mean	9.4	0.4	0.3	0.0	8.5	1.3	0.6	0.0
		±S.D.	0.7	0.7	0.5	0.0	1.2	1.0	0.5	0.0
	Ph. 2b	Mean	8.5	0.4	0.8	0.0	6.1 ^x	1.6	1.0	1.3 ^{cz}
		±S.D.	1.2	0.5	0.9	0.0	0.8	1.2	0.5	0.5
D	Ph. 2a	Mean	7.5	2.0	0.4	0.1	3.6 ^c	3.9 ^a	2.0 ^c	0.4
		±S.D.	0.8	0.8	0.5	0.4	0.7	1.0	0.8	0.5
	Ph. 2b	Mean	1.4 ^z	4.6 ^y	3.1 ^z	1.1 ^x	1.1 ^z	4.8	2.3	1.9 ^x
		±S.D.	0.9	1.3	1.0	0.8	1.1	1.3	0.9	0.8
J	Ph. 2a	Mean	4.1	2.8	1.6	1.5	2.1 ^b	2.8	2.9	2.3
		±S.D.	0.6	0.5	1.1	0.8	1.2	0.7	1.1	1.3
	Ph. 2b	Mean	1.9 ^z	2.9	1.8	3.8 ^y	0.5 ^a	1.0	1.9	6.6 ^{cz}
		±S.D.	0.8	1.2	0.7	1.0	0.5	1.2	0.8	1.1

The numbers illustrate the incidence of each of the four types of MR. Ten consecutive MR episodes were identified during phase 2a and 2b of the MMC in the given small intestinal region and classified into the types during the experiments without feeding and during experiments with feeding.

Explanations: Groups 1-4 – MR types. Ph. 2a – phase 2a of the migrating myoelectric complex (MMC). Ph. 2b – phase 2b of the MMC. DB – duodenal bulb. D – duodenum. J – jejunum. Means±S.D., n=8. Statistical significances: ap<0.05, bp<0.01, cp<0.001 vs. relevant value obtained from the experiments without feeding; xp<0.05, yp<0.01, zp<0.001 vs. relevant value obtained during phase 2a of the MMC. Other explanations as in the section Material and Methods

3 and 4, as compared with the relevant values of the experiments without feeding. In the course of phase 2b of the MMC, the number of the jejunal MR type 1 was significantly reduced after feeding and this result occurred mostly at the expense of the number of the MR type 4 that was significantly elevated after feeding as compared with the results of the experiments in which no feeding procedure was applied (Table 2). Some effects of the MMC phase upon the number of various types of the MR pattern were also observed in this region of non-fasted rams. In the duodenal bulb of the fed animals, the number of the MR type 1 was slightly reduced during phase 2b in comparison with phase 2a of the MMC. The result occurred at the ex-

pense of increased number of the MR type 4 (Table 2). In the duodenum of not fed rams, the number of the MR type 1 was markedly lowered during phase 2b in comparison with that during phase 2a of the MMC and the result occurred at the expense of significantly increased numbers of the MR type 1, 2 and 3. In the duodenum of fed animals, the number of the MR type 1 was significantly lower during phase 2b than during phase 2a of the MMC at the expense of the greater number of the MR episodes type 4 (Table 2). In the jejunum of not fed rams, the number of the MR type 1 was significantly smaller during phase 2b than during phase 2a of the MMC. This result occurred at the expense of the greater number of the MR type 4.

Table 3. The amplitudes of the MR-forming spike bursts in the duodenal bulb, duodenum and jejunum of rams observed during phase 2a or 2b of the MMC in various feeding conditions.

			F A S T E D				N O T F A S T E D			
			no feeding		feeding		no feeding		feeding	
			first	last	first	last	first	last	first	last
DB	Ph. 2a	Mean	139	134	120	126	129	136	117	123
		±S.D.	21	17	11	15	19	18	12	13
	Ph. 2b	Mean	128	124	139x	136	140	148	137x	146x
		±S.D.	16	18	12	14	16	17	14	12

D	Ph. 2a	Mean	104	108	116	122	101	104	109	107
		±S.D.	8	10	11	12	9	8	13	15
	Ph. 2b	Mean	121	126x	101	104ax	135z	148z	106c	111c
		±S.D.	14	11	9	9	11	11	12	8

J	Ph. 2a	Mean	118	113	108	109	106	105	110	112
		±S.D.	11	10	7	10	7	8	11	10
	Ph. 2b	Mean	125	120	111	114	124x	126x	109	111a
		±S.D.	13	8	11	9	11	10	12	8

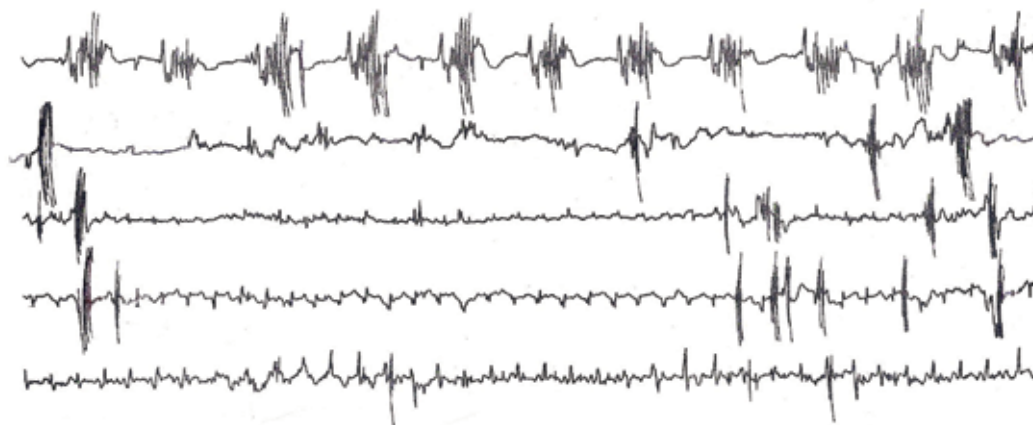
In each group of the experiments and observation period, and in the first and last MR episode of each series of the MR analysed, the amplitude of the most prominent spike within the MR-spike burst was measured.

Explanations: first – the first MR episode of the given MR episode series analyzed here; last – the last MR episode of the given MR episode series analyzed. Ph. 2a – phase 2a of the migrating myoelectric complex (MMC). Ph. 2b – phase 2b of the MMC. DB – duodenal bulb. D – duodenum. J – jejunum. Values expressed in μV . Means \pm S.D., n=8. Statistical significances: ap<0.05, cp<0.001 vs. relevant value obtained from the experiments without feeding; xp<0.05, zp<0.001 vs. relevant value obtained during phase 2a of the MMC.

Other explanations as in the section Material and Methods

Figure 2. The ‘minute rhythm’ in small bowel of fasted ram. The figure presents the fragment of the record obtained from the same sheep as Fig. 1. The mid period of phase 2a of the migrating myoelectric complex is shown. Two well-organized propagated ‘minute rhythm’ episodes are presented. The presence of the ‘minute rhythm’ in abomasal antrum and more distal jejunum and of the third pattern episode in the duodenojejunum is uncertain.

Other explanations and comments as in the legend to Figure 1.



In the jejunum of fed animals, the number of the MR type 1 was not significantly lower during phase 2a as compared with that obtained during phase 2b of the MMC and this effect was accompanied by significantly greater number of the MR type 4 (Table 2).

In the duodenum, the spike burst amplitudes were significantly lower during phase 2b after feeding in both fasted and non-fasted rams, as compared with the relevant results of the experiments without feeding (Table 3). In the jejunum, these values were also lowered, although significant change was achieved during phase 2b of the MMC only in non-fasted animals. In the duodenal bulb, after feeding, the MR amplitudes were significantly higher during phase 2b as compared with those during phase 2a of the MMC. These alterations were observed both in fasted and non-fasted rams (Table 3). In the duodenum of both fasted and non-fasted animals, the MR amplitudes were significantly higher during phase 2b than during phase 2a of the MMC. These changes were denoted both without and after feeding. In the jejunum of non-fasted rams, the MR amplitudes were significantly higher during phase 2b than during phase 2a of the MMC, but only in the experiments conducted without feeding (Table 3).

The alterations in the MR-forming spike bursts, observed in the conditions designed in the present study, were not much different from the changes in the other spike bursts (data not shown).

DISCUSSION

The results obtained in this study provide the portion of new and precise data further characterising the MR pattern in sheep. This phenomenon seems to be very variable. This event was clearly but incompletely described in this species (Fleckenstein et al., 1982; Romański, 2002; Romański, 2003; Romański, 2007a; Romański, 2009a). It was also found in other own studies on sheep further confirming its frequent appearance (Romański, 2004; Romański, 2007b; Romański, 2009b; Romański, 2010). Furthermore, similar events, not identified explicitly as the MR, were found mostly in sheep (Bueno and Ruckebusch, 1979; Gregory et al., 1985; Grivel and Ruckebusch, 1972; Lester and Bolton, 1994; Poncet and Ivan, 1984; Ruckebusch, 1970; Ruckebusch, 1989), but also in man, dog and cattle (Andrews, 2001; Bühner and Ehrlein, 1989; Castedal et al., 1998; Defilippi, 2007; Hasselbrack and Thomas, 1961; Ooms and Oyaert, 1978; Summers and Dusdieker, 1981; White et al., 1983). All the events could represent the MR pattern. Their infallible identification could be difficult without precise MR definition. In turn, it appears that such the definition cannot be proposed without more precise characterisation of the pattern enabling to elaborate more precise criteria what could also help to assess further its physiological roles and controlling mechanisms. Furthermore, without precise criteria, the normal and abnormal MR pattern cannot be satisfactorily distinguished.

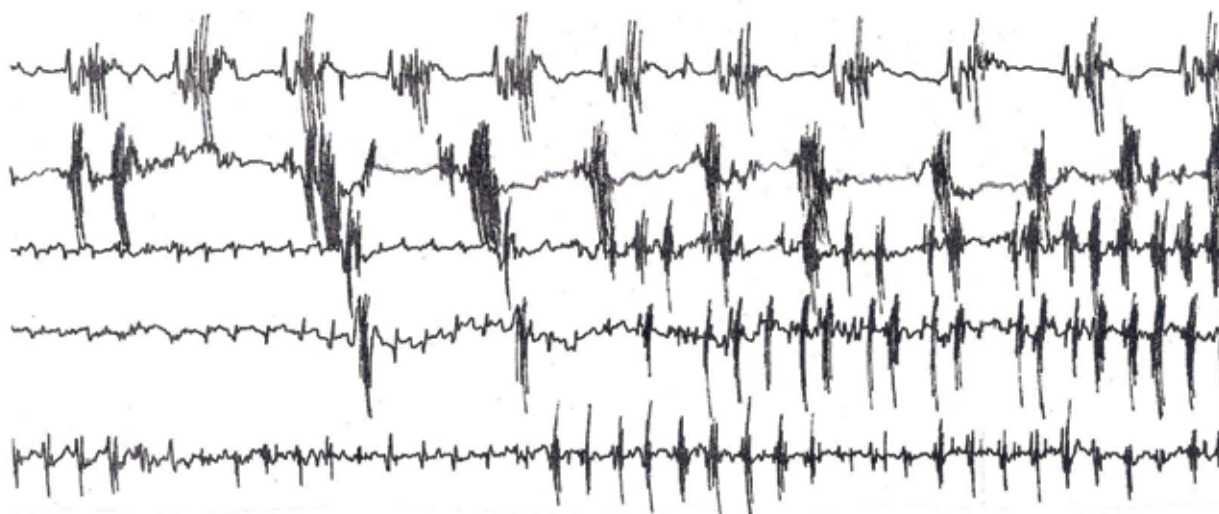
The presented results showed that during phase 2b of the MMC and after feeding, the frequency of the MRs containing more than one spike burst, was higher than those of type 1. This can apparently result from the hormonal actions. As it has been reported, such hormones like gastrin, cholecystokinin, pancreatic polypeptide, neurotensin and perhaps also neuropeptide Y contribute to the arrival of the fed pattern (Behrns and Sarr, 1994; Ledebor et al., 1999; Soffer and Adrian 1992; Thor et al., 1982). The action of these hormones can have three directions: moderate reduction of the gastrointestinal motility and transit, initiation of stationary and other local contractions, as well as overall control of the motility coordination during this period. The alterations in the release and actions of these hormones are related primarily to the changes of the situation in the intestinal lumen and are dependent mostly on the volume and composition of the chyme.

It was demonstrated that in some monogastrics, feeding disrupts the MMC pattern thus inducing more irregular fed pattern resembling phase 2 of the MMC (Kerlin and Phillips, 1982; Sarna, 1985). In the small bowel, the fed pattern contained usually more frequent contractions, but their amplitude was lower (Ahluwalia et al., 1994; Bühner and Ehrlein, 1989; McCoy

and Baker, 1968; Sarna et al., 1989). The response to food is, however, not uniform and may vary in dependence upon the various factors including nutrient composition and caloric load (Defilippi, 2003; Schönfeld et al., 1998; Schwartz et al., 2001). In sheep, the effects of feeding on the incidence and amplitude of the spike bursts (contractions) are not much different in the small bowel from the monogastrics (Bueno et al., 1977; Fioramonti and Bueno, 1988; Lester and Bolton, 1994; Romański, 2003; Ruckebusch and Bueno, 1977). It could be expected that the alterations in the MR are similar to the changes in the other spike bursts as it was observed in the present study. Feeding, as the natural and strong stimulus, enhances the gastrointestinal motility, but regional differences of this effect can be marked (Fioramonti and Bueno, 1988; Granger et al., 1985; Heddle et al., 1993; Kerlin and Phillips, 1982; Lester and Bolton, 1994). When in the small bowel feeding increases the incidence of contraction and decreases their strength, it appears that the stimulation is not maximal. Decreased amplitude of contractions after feeding may result from the volume and viscosity of the intestinal content (Malbert and Ruckebusch, 1988). The presence of the MR variability suggests that the character of the pattern can be considerably modulated according to the local requirements what guarantees the optimal conditions

Figure 3. The 'minute rhythm' in small bowel of fasted ram. The figure presents the fragment of the record obtained from the same cycle of the migrating myoelectric complex as in Fig. 2. Terminal part of phase 2b and beginning of phase 3 of the migrating myoelectric complex is shown. Four episodes in the duodenum and two well-organized propagated 'minute rhythm' episodes in the duodenojejenum can be seen. The pattern frequency (intensity) is high. The identification of the 'minute rhythm' in abomasal antrum and in more distal jejunum is not possible.

Further explanations as in the legend to Figure 1.



for the digestive and absorptive processes in the gut lumen. The MR exhibits most often the propagated character what suggests that it regulates propulsion of the digesta. Therefore, its presence not only during the digestive state, but also during the interdigestive state is desired since the flow of digesta also occurs during this period (Bueno et al., 1975). In sheep, the MR occurs both in the interdigestive and digestive state as well. The passage of digesta along the gastrointestinal tract is almost continuous in this species (Ruckebusch, 1988). As it was demonstrated in the present study, the MR incidence during the MMC cycle is not uniform. It is the lowest at the beginning of phase 2a and the highest during terminal phase 2b of the MMC. The digesta flow during both phase 2a and 2b of the MMC have not been measured, but it might be expected that it is faster during the latter subphase. Thus the digesta flow could be related to the intensity of propulsive contractions, mostly related to the MR pattern. No MR is present during phase 1, although reduced flow of digesta also occurs during this phase (Bueno et al., 1975). Therefore, we can assume that the MR may accelerate flow of digesta, but it cannot

be entirely responsible for this phenomenon. However, the propulsion in the ovine small bowel is faster during phase 2 than even during phase 3 of the MMC (Bueno et al., 1975) what further increases the putative role of the MR.

CONCLUSIONS

The results indicate that the MR exhibits high variability of its frequency (intensity) and also propulsivity. The variable number of the spike bursts in one MR episode allowed to distinguish some types of the pattern. The character of the MR was modulated by feeding conditions and was dependent upon the MMC phase.

Finally, it can be concluded that high variability of the MR comprises its character and intensity (strength) and might be related to the intraluminal milieu in the gut as well as the controlling mechanisms. The physiological role of the MR in the digesta propulsion during both the digestive and interdigestive states can be postulated. ■

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