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The diversity of 'minute rhythm' forms in the ovine small bowel: relationship to feeding and to the phase of the migrating myoelectric complex

Krzysztof W. Romański*

Department of Biostructure and Animal Physiology, Faculty of Veterinary Medicine, Wrocław, University of Environmental and Life Sciences, Wrocław, Poland

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ABSTRACT

The precise character of the 'minute rhythm' (MR), the common motility pattern occurring mostly in the small bowel, still remains to be elucidated. Since more complete information in this area can help to assess its physiological meaning and roles, myoelectrical recordings were performed in six rams equipped with bipolar serosal electrodes attached to the antral, bulbar, duodenal and jejunal (two electrodes) wall. In fasted and non-fasted rams, at least one full cycle of the migrating myoelectric complex (MMC) was recorded without and after feeding in long-term experiments. The MR patterns were identified by recordings of myoelectrical activity. Food was administered during phase 2a or 2b of the MMC. The MR incidence and coordination were evaluated in four 5-minute periods. In the pyloric (abomasal) antrum, the MR was rarely observed in fasted and non-fasted animals, while after feeding, its identification was erratic. However, in fasted animals the incidence of the MR in the antrum was significantly higher during phase 2b compared with phase 2a of the MMC. Its incidence was significantly higher in the duodenum during phase 2b compared with phase 2a of the MMC in non-fasted rams, before and after feeding. In the duodenal bulb and the duodenum, the pattern was most frequently observed independently of feeding conditions. In the jejunum, one MR cycle usually comprised more than one or two spike bursts, so that when the myoelectric activity was more intense, its identification was sometimes uncertain. The MR was often absent on the distal jejunal recording channel. In the upper segments examined the MR was the most distinct and migrated regularly between adjacent sites. During phase 2b, the MR incidence was slightly higher than during phase 2a of the MMC. Feeding increased MR incidence significantly, but these changes were more evident during the initial observation periods. It was concluded that the diversity of MR is high which may result, at least in part, from the limited influence of feeding and the MMC phase upon the pattern.

Key words: ram, abomasal antrum, duodenal bulb, duodenum, jejunum, migrating myoelectric complex, minute rhythm, fasting, feeding

*Corresponding author:

Prof. dr hab. Krzysztof W. Romański, Department of Biostructure and Animal Physiology, Faculty of Veterinary Medicine, Wrocław University of Environmental and Life Sciences, Norwida 31, 50-375 Wrocław, Poland, Phone: +48 71 320 5422; E-mail: krzysztof.romanski@up.wroc.pl

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Introduction

The rhythmic myoelectrical spiking activity, occurring at approximately 1-minute intervals, was observed initially in sheep by RUCKEBUSCH (1970) and it was then found in the human small intestine in the late 1970’s. The pattern was called the ‘minute rhythm’ (MR) (FLECKENSTEIN and ØIGAARD, 1978). This motility pattern was also identified as ‘migrating clustered contractions’ or ‘discrete clustered contractions’ (SARNA and OTTERSON, 1989). A few years later, after it was discovered in humans, the pattern was described in the small bowel of various animal species, including sheep (FLECKENSTEIN et al., 1982). MR was identified in relation to other myoelectric events, especially to the migrating myoelectric complex (MMC) and was found mostly during its phase 2 (SZURSZEWSKI, 1969). Despite the fact that it was known that spiking activity represents myoelectric correlates for mechanical contractions, the presence of the contractile counterpart of MR was confirmed by mechanical recordings, initially in pigs (FLECKENSTEIN et al., 1982). Some years later, simultaneous myoelectric (electrodes) and mechanical (strain gauges) recordings confirmed it also in sheep (ROMAŃSKI, 2004; ROMAŃSKI, 2007). In several studies in sheep, characterization and thus the physiological meaning and role of the MR have been defined, but this is still far from being complete (FLECKENSTEIN et al., 1982; ROMAŃSKI, 2002; ROMAŃSKI, 2003; ROMAŃSKI, 2009). Although its occurrence, migratory character, total duration and some other parameters have been presented initially (FLECKENSTEIN et al., 1982; ROMAŃSKI, 2002), as well as its partial dependence upon the cholinergic and cholecystokinin-dependent mechanisms (COLLMAN et al., 1983; ROMAŃSKI, 2002; ROMAŃSKI, 2007; ROMAŃSKI, 2009), extensive effort is still necessary to provide a satisfactory scientific explanation. This also involves a description of the possible forms of MR, the role of feeding, and the influence of the MMC phase upon the pattern. Apart from some studies in humans and various animal species, including sheep, this information still remains fragmentary. Thus, the aim of this study was to present more detailed characteristics of MR, including the incidence of MR in the ovine antrum, duodenal bulb, the duodenum, and jejunum during phase 2a and phase 2b of the MMC, in various feeding conditions.

Materials and methods

Six healthy rams of the Polish Merino breed, each weighing 38-43 kg, were used in the study. Before the experiments, the animals were kept in a natural light cycle and fed with good quality hay and grain mixture. Drinking water was continuously available.

Animal preparation. The rams underwent the surgical procedure as described in detail previously (for example: ROMAŃSKI, 2003). In brief, in fasted, anesthetized and laparotomized animals, five bipolar electrodes were sewn from the outside onto the abomasal antrum (4 cm above the pyloric ring), bulbar (6 cm below the pyloric ring), duodenal (50 cm below the pyloric ring) and jejunal (two electrodes located 250 cm - called here as upper jejunum and 350 cm - called as lower jejunum, below the pyloric ring). The marked wires were exteriorized and fixed to the skin with the plug. Drinking water was always available. Feeding began two days after the surgery and was gradually intensified.

Experimental procedure. Randomized experiments were started about two weeks following the surgery. A total of 36 basal experiments and three additional experiments, each lasting 2.5-5 hours, were performed on six either 48-h fasted or non-fasted rams. Six preliminary experiments lasted 1.5-2 hours each. They were conducted to confirm the correct electromyographical recordings. Drinking water was available just before and just after the experiments, and during the inter-experimental periods. In the course of each experiment, including preliminary experiments, at least one full MMC cycle was recorded after the short initial recording period. Two main groups of experiments were conducted. The first group was in fasted rams, with and without feeding. The second group of experiments in non-fasted rams was performed with and without feeding. The MMC and MR patterns were identified in all the tracings obtained. Since in one experiment performed in fasted sheep without feeding, no MR was observed; this experiment was excluded and an additional similar experiment was performed in the same ram on the next day. In both non-fasted and unfed rams, MR was absent in two experiments. Therefore, two additional similar experiments were performed on the same sheep, on separate days. During all the experiments performed, the myoelectric activity was continuously recorded using an electroencephalograph (Reega Duplex TR XVI, Alvar Electronic, Montreuil, France). The time constant was adjusted to 0.01s, speed of paper was 2.5 cm/s, and the maximum filter position was also designed. Feeding during the experiment contained 250 g of the grain mixture. It was started 2-5 min following the onset of a given MMC subphase and lasted 2-3 min.

Electromyographical recordings. In all the obtained electromyographical recordings, the MMC cycles (CODE and MARLETT, 1975) were identified, including division of phase 2 into phases 2a and 2b MMC (DENT et al., 1983; ROMAŃSKI, 2002). The MMC was defined as a recurring pattern containing three or four phases. Phase 1 - the relative lack of spike bursts, phase 2 - increased, irregular spike burst intensity, phase 3 - the maximal spike burst intensity, phase 4 decreasing irregular spike burst intensity, before phase 1 of the next MMC cycle. During phase 2b, spike burst intensity was greater than during phase 2a, usually with a clear border between both sub-phases. During these MMC phases, MR was identified in all segments examined, i.e. in all recording channels, whenever it was possible. The pattern was defined as single spike burst or as the group of spike bursts arriving more or less regularly, in time intervals lasting around one minute, in one or more segments examined. The number of MRs was counted in four 5-minute periods (periods

1-4) of phase 2a or phase 2b of the MMC and expressed in cycles per minute (cpm). After the termination of period 4, the MMC phase remained the same as during period 1. The percentage of the MR cycles present in at least three consecutive channels of the total number of MRs was also calculated during these periods. The first period of MR analysis was started 2-5 minutes after clear MMC phase identification (initial period), or directly after termination of feeding.

Data elaboration. All the values in the groups were statistically elaborated and the mean values with standard deviations were calculated. Then, the statistical significances were determined using the Student t-test for paired values and the Wilcoxon signed rank test (SNEDECOR and COCHRAN, 1971), where appropriate. The t-test was preceded by variance analysis, whenever possible. Statistical significances ($P<0.05$; $P<0.01$; $P<0.001$) were determined between consecutive 5-minute periods in the given segments examined, or between the data obtained during phase 2a vs. phase 2b of the MMC.

The national (Animal Protection Bill) and local (The Statute of the Wrocław University of Environmental and Life Sciences) guidelines were followed, which are in accordance with international guidelines. The experimental model used in the study was approved by Second Local Ethical Committee in Wrocław (decision No. 87/03, signed by chief of this Committee, prof. dr hab. Roman Kołacz).

Results

In all the experiments performed, the duration of phase 2 of the MMC cycles was long enough to mark off four 5-minute periods during phase 2a and four 5-minute periods during phase 2b of the analyzed cycles. The total duration of each MMC cycle studied far exceeded 60 min.

MR incidence. In the antrum, MR was identified sparsely, but its identification was clear in fasted or non-fasted animals, that is, without feeding (Fig. 1, Tables 1, 2). After feeding, when antral spike bursts were more intense, identification of MR was uncertain. In the duodenal bulb, the MR pattern occurred more frequently than in the antrum (Tables 1, 2) and - as in the antrum - it comprised mostly single spike bursts, especially in fasted animals. In the duodenum, the occurrence of the MR was most regular and frequent (Tables 1, 2). In the upper jejunum, the pattern incidence was less frequent (Tables 1, 2). Sometimes its identification was difficult in this segment since it usually comprised more than one spike burst in one MR cycle. In the lower jejunal region examined, the MR was usually absent or erratic (Fig. 1). Therefore, it was often not possible to identify it precisely.

The effects of the MMC phase and feeding. The MR incidence was slightly higher during phase 2b than during phase 2a of the MMC (Tables 1, 2). The greatest differences were observed after feeding (Table 1). There were no marked differences in MR incidence during consecutive 5-minute periods, whether during phase 2a or 2b of the MMC in fasted animals. Feeding increased MR incidence significantly in all the experiments, but these changes were most evident during the first two periods after feeding (Tables 1, 2).

Table 1. The incidence of the ‘minute rhythm’ in fasted rams, before and after feeding, during phase 2a and phase 2b of the migrating myoelectric complex (MMC)

			Pyloric antrum				Duodenal bulb				Duodenum				Proximal jejunum			
			1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
FAST	2a	Mean	0.0	0.1	0.0	0.0	0.3	0.3	0.3	0.2	0.6	0.6	0.6	0.7	0.1	0.2	0.2	0.4
		± SD	0.0	0.1	0.1	0.0	0.2	0.3	0.3	0.3	0.2	0.1	0.1	0.1	0.2	0.2	0.3	0.2
	2b	Mean	0.1	0.0	0.2^{xa}	0.1^{x}	0.4	0.4	0.4	0.5	0.7	0.7	0.7	0.7	0.3	0.4	0.4	0.5
		± SD	0.1	0.1	0.0	0.1	0.3	0.3	0.3	0.4	0.1	0.1	0.1	0.1	0.2	0.3	0.2	0.2
FED	2a	Mean					0.4	0.3	0.3	0.3	0.7	0.6	0.6	0.7	0.5	0.4	0.3	0.4
		± SD					0.3	0.3	0.3	0.3	0.1	0.2	0.2	0.1	0.2	0.2	0.2	0.2
	2b	Mean					0.6	0.5	0.6	0.6	1.2^{z}	1.1^{z}	0.9^{ya}	0.9^{xa}	0.6	0.4	0.4^{a}	0.4^{a}
		± SD					0.5	0.4	0.5	0.5	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.2

Values represent the number of MR patterns identified during the given 5-minute period. 2a: phase 2a of the MMC, 2b: phase 2b of the MMC. 1 - 4: consecutive 5-minute periods; means ± SD, n = 6. Statistical significances: $^{x}P<0.05$, $^{y}P<0.01$, $^{z}P<0.001$ vs. relevant value from phase 2a MMC; $^{a}P<0.05$, $^{b}P<0.01$ vs. relevant value from the period 1. Further explanation as in the chapter Materials and methods.

Table 2. The incidence of the ‘minute rhythm’ in non-fasted rams, before and after feeding during phase 2a and phase 2b of the migrating myoelectric complex (MMC)

			Pyloric antrum				Duodenal bulb				Duodenum				Proximal jejunum			
			1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
NOT FED	2a	Mean	0.0	0.0	0.1	0.0	0.3	0.4	0.3	0.4	0.7	0.7	0.7	0.8	0.2	0.2	0.3	0.3
		± SD	0.1	0.0	0.1	0.0	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.2
	2b	Mean	0.0	0.0	0.1	0.1	0.5^{x}	0.5	0.4	0.4	0.8	0.9^{x}	0.9^{x}	0.9	0.4^{x}	0.4	0.4	0.5
		± SD	0.1	0.0	0.1	0.1	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.2
FED	2a	Mean					0.4	0.5	0.4	0.4	0.9	0.8	0.7^{a}	0.7^{a}	0.4	0.3^{a}	0.4	0.3
		± SD					0.2	0.2	0.2	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2
	2b						0.6^{x}	0.7	0.6	0.5	1.0	0.9	0.9^{y}	0.9^{x}	0.5	0.4	0.4	0.4
							0.3	0.4	0.4	0.3	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.1

Values represent the number of MR patterns identified during the given 5-minute period. 2a: phase 2a of the MMC, 2b: phase 2b of the MMC. 1 - 4: consecutive 5-minute periods; means ± SD, n = 6. Statistical significances: $^{x}P<0.05$, $^{y}P<0.01$ vs. relevant value from phase 2a MMC; $^{a}P<0.05$ vs. relevant value from period 1. Further explanation as in the chapter Materials and methods.

Table 3. The percent of ‘minute rhythm” cycles in the duodenum

			Duodenal bulb				Duodenum				Proximal jejunum			
			1	2	3	4	1	2	3	4	1	2	3	4
FAST	2a	n_1	9	9	9	7	17	17	18	20	1	6	7	7
		n_2					1	6	7	7				
		%					5.9	35.3	38.9	35.0				
	2b	n_1	14	12	13	12	20	21	21	21	9	12	11	14
		n_2					19	12	11	12				
		%					95.0	57.1	52.4	57.1				
FED	2a	n_1	11	8	9	8	21	19	19	22	16	13	9	12
		n_2					11	8	9	8				
		%					52.4	42.1	47.4	36.4				
	2b	n_1	17	15	17	18	37	32	27	27	18	13	11	11n
		n_2					17	13	11	11				
		%					44.6	40.6	40.7	40.7				

Coordinated with two adjacent channels (duodenal bulb and upper jejunum) vs. the total number of occurrences of the pattern in the duodenum during 5-minute periods (n_1) in fasted rams, before and after feeding during phase 2a and phase 2b of the migrating myoelectric complex (MMC). 2a: phase 2a of the MMC, 2b: phase 2b of the MMC; n_2: number of minute rhythm episodes in the duodenum coordinated with two adjacent channels (duodenal bulb and upper jejunum). 1 - 4: consecutive 5-minute periods. Further explanation as in the chapter Materials and methods.

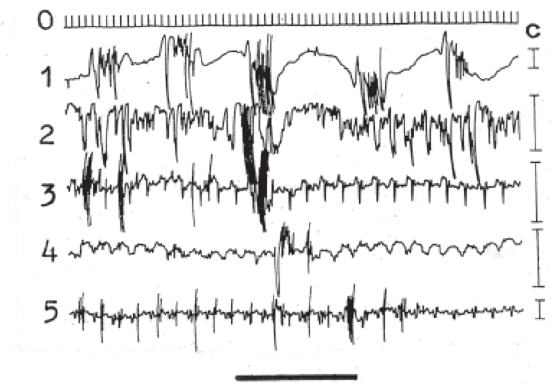

Fig. 1. Two evident episodes of the minute rhythm (MR) starting from the abomasal antrum in fasted sheep and migrating down towards the jejunum

Their boundaries are marked with horizontal bars. In the upper jejunum it is visible, despite the other spike bursts nearby. In the lower jejunum, the first MR episode is blurred because of the presence of a longer spike burst series, while the second MR episode terminated in the upper jejunal recording channel. 0 - time in seconds, 1 - abomasal antrum, 2 - duodenal bulb, 3 - duodenum, 4 - upper jejunal site, 5 - lower jejunal site, c - calibration 50 μV. Further explanation as in the chapter Materials and methods.

Table 4. The percent of 'minute rhythm" cycles in the duodenum

			Duodenal bulb				Duodenum				Proximal jejunum			
			1	2	3	4	1	2	3	4	1	2	3	4
NOT FED	2a	n_1	4	7	6	6	20	21	22	22	6	6	9	10
		n_2					4	6	6	6				
		%					20.0	28.6	27.3	27.3				
	2b	n_1	10	10	9	7	24	26	26	27	12	11	12	14
		n_2					10	10	9	7				
		%					41.7	38.5	34.6	25.9				
FED	2a	n_1	11	12	10	9	27	24	22	22	12	9	13	9
		n_2					11	9	10	9				
		%					40.7	37.5	45.0	40.9				
	2b	n_1	14	20	16	15	31	26	26	26	13	12	11	11
		n_2					13	12	11	11				
		%					41.9	46.2	42.3	42.3				

Coordinated with two adjacent channels (duodenal bulb and upper jejunum) vs. the total number of occurrences of the pattern in the duodenum during 5-minute periods (n_1) in non-fasted rams, before and after feeding during phase 2a and phase 2b of the migrating myo- electric complex (MMC). 2a: phase 2a of the MMC, 2b: phase 2b of the MMC; n_2: the number of minute rhythm episodes in the duodenum coordinated with two adjacent channels (duodenal bulb and upper jejunum). 1 - 4: consecutive 5-minute periods. Further explanation as in the chapter Materials and methods.

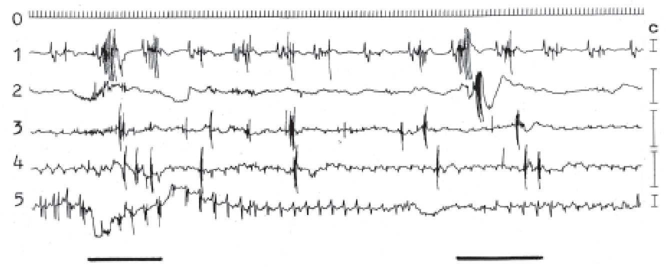

Fig. 2. One episode of the minute rhythm (MR) starting from the abomasal antrum in fasted sheep and migrating towards the jejunum

In the upper recording channels its propagation is difficult to assess. In the lower jejunum its clarity is diminished because of the presence of accompanying spike bursts nearby. Explanation as in Fig. 1 caption.

MR coordination. MR coordination exhibited a migratory (propagated MR) or non-migratory character. Sometimes the character of MR coordination was difficult to define precisely (Fig. 2). The percentage of MR cycles occurring in at least three consecutive electrode position sites, i.e. coordinated in the duodenal bulb, the duodenum and the upper jejunum, usually oscillated around 35-50 % (Tables 3, 4). It was higher during phase 2b than during phase 2a of the MMC, especially in the experiments without feeding. When feeding was offered in the course of phase 2a, the values were higher than during phase 2b of the MMC (Tables 3, 4).

Discussion

The obtained results exhibit the high diversity of the MR forms in the ovine small intestine, regarding the basic features of the pattern, including its occurrence in a given gastrointestinal segment, its incidence, and propulsivity. It is also dependent on the animal species examined, the site of occurrence (i.e. the gastrointestinal segment or another organ), and feeding conditions, as shown in the *in vivo* and *in vitro* studies (FLECKENSTEIN et al., 1982; FLECKENSTEIN and ØIGAARD, 1978; LÜDTKE et al., 1991; PRIMI and BUENO, 1987; QUIGLEY et al., 1984; RIEMER et al., 1977; ROMAŃSKI, 2002; WILMER et al., 1998). The presented observation of two groups of MR, propagated or non-propagated, has been confirmed previously (BORTOFF et al., 1984; FLECKENSTEIN et al., 1982; ROMAŃSKI et al., 2001).

In the present study, MR was observed infrequently in the antrum. It has also been noticed there in other animal species, but not in all species studied (BORTOFF et al., 1984; FLECKENSTEIN et al., 1982; FLECKENSTEIN and ØIGAARD, 1978). This observation further confirms that the pattern, while present in the antrum, migrates towards the duodenum through the pylorus. It is currently difficult to identify the antral MR after feeding, which is in accordance with the observations by BUENO and FIORAMONTI (1980) who proposed that the pattern could be observed only in food-restricted sheep. This also seems to be in accordance with the observations that increased antral spiking activity after feeding can make MR less visible. The information provided by FLECKENSTEIN et al. (1982), that in sheep the antral MR does not migrate to the duodenum is, however, in conflict with the present and previous results, since almost all MR patterns observed migrated to the duodenum (see also the examples: ROMAŃSKI, 2002; ROMAŃSKI, 2003; ROMAŃSKI, 2009).

In the obtained recordings, the MR was most frequently observed in the duodenal bulb and duodenum, as well as in the upper jejunum, which is not different from the observations made by FLECKENSTEIN et al. (1982) in various animal species, including sheep. The authors stated that the MR was most marked in the proximal small bowel. However, in the jejunum, the MR usually differed from that in the duodenum. It contained more than 1-2 spike bursts in one pattern, which might decrease its clarity, especially when the neighboring spiking activity is more intense. In the lower parts of the jejunum, this was even more pronounced and, quite frequently, the MR was virtually absent there, not only in this study (as in the examples, see: ROMAŃSKI, 2002; ROMAŃSKI, 2004).

Not all the authors could confirm the presence of MR in these areas (FLECKENSTEIN et al., 1982; FLECKENSTEIN and ØIGAARD, 1978). Therefore, the suggestion of SARNA and OTTERSON (1989) that the MR migrates over short distances appears to be correct, at least in part.

The MMC phase and feeding conditions may cause important MR alterations, further increasing the diversity of the pattern and making its precise definition more difficult. This also suggests its various possible physiological role, although the role of the MR is still unknown (WEISBRODT, 1981). It may be assumed that the physiological role of the MR is similar to the role of propagated and stationary contractions in the gut, i.e. to maintain the local transport and mixing of the digesta.

Phase 2b of the MMC exhibits more intense myoelectrical and motor activity, thus the greater MR incidence, especially the propulsive patterns, indicate not only more active motility, but also propulsion and digesta flow. It seems to be especially important in the duodenum. Since phase 2b of the MMC is quite long in sheep, the presence of more frequent migrating MR patterns facilitates the periodic transport of the digesta towards the jejunum. Due to the constant inflow of pancreatic juices and bile to the duodenum, the duodenal contents should not stay there too long.

The MR could be generally defined as a repetitive pattern occurring every 0.5-2.0 min, at least in some animal species (FLECKENSTEIN et al., 1982). In humans and pigs, its frequency oscillates between 0.5 and 1.5 min (FLECKENSTEIN and ØIGAARD, 1978; ROMAŃSKI et al., 2001). Our own observations in sheep were similar (ROMAŃSKI, 2002). This may suggest that only the repetitive pattern can be defined as MR. Thus, the question arises whether a single pattern (propulsive or not) occurring from time to time can be treated as MR. A further complication may occur when the single pattern is propulsive: it may thus resemble a peristaltic rush or even a giant migrating contraction (MELTZER and AUER, 1907; SARNA and OTTERSON, 1989).

In the present study, feeding increased MR incidence, usually during the first one or two 5-minute observation periods. This is less than could be expected in non-ruminant animals, since food remains in the simple stomach much longer than 10 minutes. In ruminants, usually deprived of interdigestive periods, and possessing such a capacious digestive chamber as the rumen, there are no marked differences between the pre-feeding and post-feeding periods. Therefore, food cannot directly stimulate either the abomasum (the proper stomach) or the duodenum, since food usually remains for a long time in the forestomachs after feeding. The effect of feeding may thus be weaker and shorter than in non-ruminant species. This may also explain the presence in sheep, unlike in dogs, of the MMC pattern after feeding as well (BUENO et al., 1975) and the relatively small differences between MR parameters in fasted and fed sheep.

Finally, it was concluded that the diversity in the MR is high and this may result, at least in part, from the limited influence of feeding and the MMC phase upon the pattern.

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SAŽETAK

Točno obilježje „minutnog ritma“ (MR), načina motiliteta osebujnog za tanko crijevo, još uvijek nije posvema razjašnjeno. Budući da više potpunih informacija na ovom području može pomoći u procjeni njegova fiziološkog značenja i uloge, poduzeto je mioelektrično snimanje na šest ovnova kojima su bipolarne elektrode stavljene na antralnu, bulbarnu, duodenalnu i jejunalnu (dvije elektrode) stijenku. U trajnim pokusima u izgladnjelih i neizgladnjelih ovnova bio je snimljen najmanje jedan potpuni krug migrirajućeg mioelektričnog kompleksa (MMK) s hranjenjem i bez hranjenja. Obilježja MR identificirana su na snimkama mioelektrične aktivnosti. Hrana je ovnovima bila dana tijekom faze 2a ili 2b MMK. Pojavljivanje MR i koordinacija bili su procjenjivani u četiri 5-minutnih razdoblja. U piloričkom (abomazalnom) antrumu MR bio je rijetko zabilježen u izgladnjelih i neizgladnjelih životinja, dok je nakon hranjenja bio nepravilan. Međutim, u izgladnjelih životinja pojavljivanje MR u antrumu bilo je značajno češće tijekom faze 2b u usporedbi s fazom 2a MMK u neizgladnjelih ovnova, prije i nakon hranjenja. U duodenalnom bulbusu i duodenumu MR je češće bio opažen neovisno o uvjetima hranjenja. U jejunumu je ciklus MR obično obuhvaćao više od jednog ili dva vrška prenapunjenosti, tako da ga se nije moglo sa sigurnošću identificirati kad je mioelektrična aktivnost bila pojačana. U distalnom jejunumu MR je često bio odsutan. U gornjim dijelovima MR je bio najizraženiji i pravilno se izmjenjivao između susjednih područja. Tijekom faze 2b, incidencija MR bila je nešto viša nego tijekom faze 2a MMK. Hranjenje je značajno povećalo incidenciju MR, ali su te promjene bile očitije u početnom razdoblju promatranja. Može se zaključiti da je raznolikost MR vrlo velika što, barem djelomično, može proizaći iz ograničenog utjecaja hranjenja i MMK faze.

Ključne riječi: ovan, abomazusni antrum, duodenalni bulbus, duodenum, jejunum, migrirajući mioelekrični kompleks, minutni ritam, gladovanje, hranjenje