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Original article

THE 'MINUTE RHYTHM' INCIDENCE IN THE OVINE ABOMASAL ANTRUM AND SMALL INTESTINE

K. W. ROMAŃSKI

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

Summary

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To characterise further the 'minute rhythm', six healthy rams were equipped with serosal electrodes sewn onto the abomasal antrum and the small bowel. The experiments were performed before and after feeding. Food was offered during phase 2a or 2b of the migrating motility complex. The 'minute rhythm' incidence and coordination were assessed during four 5-minute observation periods. In the duodenal bulb and duodenum, the pattern was observed more frequently than in other segments examined. During phase 2b, the 'minute rhythm' incidence was often more frequent than during phase 2a of the migrating motility complex. Feeding increased significantly the 'minute rhythm' incidence, but these alterations were more evident during first two observation periods. In the jejunum, duration of one 'minute rhythm' episode was longer than in more proximal segments. In the more distal jejunal recording site the 'minute rhythm' was often absent. The pattern was well coordinated mostly in the antroduodenum and its propagation velocity was the highest also in the upper small bowel. It is concluded that the 'minute rhythm' incidence, form, and coordination depended upon the feeding conditions, intensity of intestinal motility and the gastrointestinal segment.

Key words: abomasal antrum, feeding, migrating motility complex, minute rhythm, sheep, small intestine

INTRODUCTION

The rhythmic myoelectrical spiking activity was observed quite early in sheep, during *in vivo* studies (Ruckebusch, 1970; Grivel & Ruckebusch, 1972). Few years later, Fleckenstein & Øigaard (1978) identified this pattern in man and called it the 'minute rhythm' (MR). The MR was considered as the repeatable spike bursts arriving in about one minute period. It was also identified in some other animal species including dog, cat rabbit and pig (Fleckenstein *et al.*, 1982). Its physiological role is uncertain, although its presence may facilitate digesta transport and keep the gut active, either in men or in animals. The MR was observed during the active irregular phases of another myoelectric activity pattern, i.e. the migrating motility

complex (MMC). The MMC cycle also occurs in several species including sheep and represents the periodical event composed of 3-4 phases (Szurszewski, 1969; Bueno *et al.*, 1975; Code & Marlett, 1975). Phase 1 of the MMC contains no or almost no spiking and contractile activity. These activities gradually intensify during phase 2 and are the maximal during phase 3 of the MMC. The transient phase 4 of the cycle is not always observed. Despite over 40 years overpassing from the discovery of the MMC, the knowledge regarding its occurrence and control is still incomplete (Takahashi, 2013; Deloose *et al.*, 2015). The mechanical correlates of the MR were also presented (Romański, 2009a). In sheep, the pattern was found mostly in the small bowel. Its occurrence, migratory character, total duration and some other parameters were unsufficiently described so far (Fleckenstein *et al.,* 1982; Romański, 2002). It appears to be very variable since the species differences have been poorly recognised. However, for its more precise characterisation, further extensive studies are desirable and obtained results can be useful in better understanding its physiological importance and roles within the digestive system.

Thus, the aim of this work was to present further MR characteristics, including its incidence and coordination in the abomasal antrum, the duodenal bulb, the duodenum, and the jejunum of non-fasted rams during phase 2a and 2b of the MMC, before and after feeding.

MATERIALS AND METHODS

Animals

Six adult rams of Polish Merino breed, each weighing 38–44 kg, were used. Before the experiments, the animals were fed with hay and grain mixture with free access to the drinking water. Details of this experimental model were already published (Romański, 2003).

Animal preparation

All the rams underwent surgical procedure. Briefly, in 24 h-fasted, anesthetised animals (Romański, 2006), midline laparotomy was performed and five bipolar electrodes were attached from the outside onto the abomasal antrum (4 cm above the pyloric ring), the duodenal bulb (6 cm below the pyloric ring), the duodenum (50 cm below the pyloric ring) and the jejunum (first jejunal electrode located 250 cm below the pyloric ring was qualified as 'jejunum I' and second jejunal electrode spaced 100 cm distally from 'jejunum I' was called 'jejunum II'). Drinking water was available before and after the surgery. Feeding was started gradually two days following the surgical procedure.

Experimental design

The randomised experiments were initiated approximately two weeks after the postsurgical recovery. Two hours before the experimental onset, food was removed from the cage. The total of 18 experiments each lasting 3–5 hours were conducted on six rams, with or without feeding. During the experiments performed in this study, the myoelectric activity was continuously recorded from all recording sites using an electroencephalograph (Reega Duplex TR XVI, Alvar Electronic, Montreuil, France). The MMC and MR patterns were detected during the experimental recordings. During each experiment, at least one full MMC cycle was recorded after the initial short recording period. In all rams three groups of the experiments were performed. In the first group, the experiments were done without feeding. In the second group of the experiments, the rams

were fed during phase 2a of the MMC. In the third group, the animals were fed during phase 2b of the MMC. Feeding dring the experiment consisted in 250 g of the grain mixture. It was started 2–5 min following the onset of given phase and lasted 2–3 min.

Electromyographical recording analysis

The MMC cycles were identified (by visual inspection) upon all the electromyographical recordings, including the division of phase 2 of the MMC into phase 2a and 2b (Dent *et al.,* 1983; Romański, 2002). The MMC was defined as the regularly recurring pattern containing three or four phases (Bueno *et al.,* 1975; Code & Marlett, 1975). Phase 1 represents the relative lack of the spike bursts, phase 2 arrives as increased irregular spike burst intensity, phase 3 represents the cohort of the maximal spike bursts, terminal phase 4 is of decreasing intensity irregular spike burst period. In the course of phase 2b, the spike burst intensity was greater than during phase 2a of the MMC. The visible step occurred usually between both these phases. During both MMC phases, the MR was usually identified in the recording channels. The pattern was generally defined as the single spike burst or as the group of spike bursts arriving more or less regularly at time intervals lasting around one minute and observed in one or more segments examined (electrode positions of the recording channels). The number of MR events was counted in four 5-minute observation periods numbered consecutively from 1 to 4, in the course of phase 2a or 2b of the MMC. Since the total duration of MMC cycles well exceeded 70 min, these phases were long enough to distinguish these observation periods. The numbers of MR present in the given recording channel (without jejunum II) and the percentage of MR cycles migrating to the next recording channel were determined and calculated in all recording channels, except the jejunum (too erratic MR episodes), during the observation periods. The first period of MR analysis was started 2–5 minutes after clear MMC phase identification in the experiments without feeding. In the remaining experiments it began just after the termination of feeding. Propagation velocities were calculated in each experiment performed in fed or not fed rams for clear single MR patterns propagated from the duodenal bulb to the duodenum, from the duodenum to the jejunum I and from the jejunum I to the jejunum II.

All studies have been approved by the II Local Ethical Committee for Experimental Animals in Wrocław and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Statistical analysis of data

The MR incidence values in all the groups studied were statistically elaborated and the mean values along with standard deviations (±SD) were calculated. Then, the statistical significances were determined using the Student t-test for paired values (Snedecor & Cochran, 1971). The t-test was preceded by the analysis of variance. Statistical significances ($P<0.05$; $P<0.01$; $p<0.001$) were determined between the 5-minute observation periods in the segments examined or between the data obtained during phase 2b and 2a of the MMC.

RESULTS

In all the experiments performed, the typical MMC cycles arrived independently of feeding conditions. The MR cycles could

Table 1. The incidence of the 'minute rhythm' (MR) episodes in the rams, before and after feeding

	P	Experiment 1 – not fed		Experiment 2 – fed during phase 2a	Experiment 3 – fed during phase 2b
		MMC phase 2a	MMC phase 2b		
Pyloric antrum	1	0.4±0.2	0.4±0.2		
	2	0.0±0.0	0.0±0.0		
	3	0.5±0.5	0.5±0.4		
	4	0.0±0.0	0.5±0.3*		
Duodenal bulb	1	1.7±1.0	2.3±1.2	2.2±1.2	2.8±1.6
	2	2.0±1.1	2.5±1.2	2.3±1.2	3.3±1.8
	3	1.7±1.0	2.0±1.1	2.0±1.1	3.0±1.7
	4	1.8±1.6	2.0±1.1	2.0±1.3	2.7±1.5
Duodenum	1	3.3±0.5	4.0±0.6	4.5±0.5	5.2±0.8
	2	3.5±0.5	4.3±0.5*	4.0±0.6	4.3±0.5
	3	3.7±0.5	4.3±0.5*	3.7±0.5[a]	4.3±0.6
	4	3.7±0.5	4.5±0.5*	3.7±0.5[a]	4.3±0.5
Jejunum I	1	1.0±0.6	2.0±0.6*	2.0±0.6	2.5±0.7
	2	1.0±0.8	1.8±0.8	1.5±0.5	2.0±0.9
	3	1.5±1.0	2.0±0.9	2.2±0.8	1.8±0.8
	4	1.7±1.1	2.3±0.8	1.3±0.4[a]	2.0±0.5*

Values represent mean±SD number (n=6) of MR patterns identified during one (1–4) of the consecutive 5-minute periods (P). 2a: phase 2a of the MMC, 2b: phase 2b of the MMC. Statistical significances: *P<0.05 vs. relevant value from phase 2a of the MMC; [a]P<0.05 vs. relevant value from the period 1. Other explanations are given in the section Materials and Methods.

also be identified upon the tracings in all the experiments performed.

MR incidence

In abomasal antrum, the MR was identified infrequently, mostly in not fed animals, in which the MR incidence in the course of the fourth period was significantly greater during phase 2b than during phase 2a of the MMC (Table 1). Occasionally, it was difficult to identify MR in this region (Fig. 1). Soon 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 abomasal antrum (Table 1). It comprised, like in antrum, mostly the single or two spikes in one spike burst (Fig. 1). In the duodenum, the appearance of the MR was most regular and frequent. The MR incidence was significantly greater during phase 2a than during phase 2b of the MMC, either in not fed or in fed rams (Table 1). In jejunum I, the pattern incidence was less frequent than in the duodenum (Table 1, Fig. 1). However, also in the jejunum during phase 2b, the MR incidence was greater, as compared with phase 2a. These changes were observed either in fed or in not fed animals. Sometimes its identification was difficult in this segment since it comprised usually more than one-two spike bursts in one MR episode. In the jejunum II the MR was usually absent or erratic (data not shown).

The effect of the MMC phase and feeding upon the MR incidence

The MR incidence was slightly higher during phase 2b than during phase 2a of the MMC. There were no marked differences in MR incidence between consecutive 5-minute observation periods either during

phase 2a or 2b of the MMC, in the course of the experiments performed without feeding (Table 1). Feeding increased markedly the MR incidence. These changes were most evident during the first two periods after feeding (Table 1). The effect of feeding was most pronounced in the duodenum (Table 1).

MR coordination

The percent of coordinated MR cycles in the antrum and theduodenal bulb was the highest (Table 2). The percentage of coordinated MR cycles between the duodenal bulb and the duodenum was also high. It usually exceeded 80% and was higher

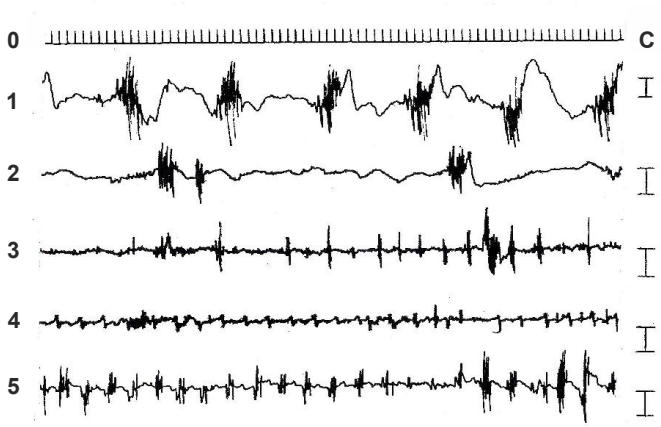

Fig. 1. Two minute rhythm (MR) episodes in the ram. In pyloric antrum, the MR recognition is not possible since its electrical activity is intense. The best, although not perfect, MR coordination is seen between the duodenal bulb and duodenum. Clear MR identification in the jejunum is not possible. 0–time in seconds; c–electrode calibration (50 μV); 1–pyloric antrum; 2–duodenal bulb; 3–duodenum; 4–jejunum I; 5–jejunum II. Other explanations are given in Material and Methods section.

Table 2. The percentage (%) of the 'minute rhythm' (MR) cycles coordinated with the next adjacent recording channel vs. the total number of the pattern episodes

			Pyloric antrum				Duodenal bulb				Duodenum				Jejunum I			
			1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Not fed	2a	n_1	1	0	3	0	10	12	10	11	20	21	22	22	6	6	9	10
		%	100	0	100	0	40	67	60	64	30	29	41	46				
	2b	n_1	1	0	2	3	14	15	12	12	24	26	26	27	12	11	12	14
		%	100	0	100	100	79	73	83	67	50	42	46	52				
Fed	2a	n_1					13	14	12	12	27	24	22	22	12	9	13	9
		%					77	79	58	75	44	38	59	41				
	2b	n_1					17	20	18	16	31	26	26	26	13	12	11	11
		%					88	100	94	94	48	46	42	46				

2a: phase 2a of the MMC, 2b: phase 2b of the MMC; n=6; n_1: the total number of MR episodes in the given recording channel. 1–4: consecutive 5-minute periods (P). Other explanations are given in the section Materials and Methods.

Table 3. Propagation velocities of the 'minute rhythm' observed in the duodenojejunum of rams, before and after feeding

	Experiment 1 – not fed		Experiment 2 – fed during MMC phase 2a	Experiment 3 – fed during MMC phase 2b
	MMC phase 2a	MMC phase 2b		
Duodenum	15.7±4.2	13.4±4.3	10.6±4.0	8.5±2.4
Duodenojejunum	12.6±5.5	10.9±4.7	7.1±3.2	6.4±5.2
Jejunum	8.3±4.0*	7.0±1.8*	4.3±2.4*[a]	2.2±3.8*[a]

Phase 2a – phase 2a of the MMC, phase 2b – phase 2b of the MMC; n=6. Statistical significances: *$p<0.05$ vs. relevant value in the duodenum; [a]$p<0.05$ vs. relevant value in not fed animals. Other explanations as in the section Materials and Methods.

during phase 2b than during phase 2a of the MMC (Table 2). This coordination exhibited migratory (propagated MR) or non-migratory (stationary) character. After feeding the decreasing tendency in MR coordination was observed.

MR propagation velocity

The propagation velocity of the MR was the highest in the duodenum (Table 3) and it was significantly higher than in the jejunum. In fed animals it was significantly slower in the jejunum than in rams without feeding. Slowing tendency was also observed in the course of phase 2b as compared with phase 2a of the MMC.

DISCUSSION

The MR was observed in sheep, in the several own studies (Romański, 2002; 2007; 2009b; 2010) and in the studies on sheep and calf reported by others (Fleckenstein *et al.,* 1982; Poncet & Ivan, 1984; Ruckebusch, 1989). Therefore, the MR represents the well-established motility pattern. The presented results have shown the marked differences in MR incidence and coordination in ovine antrum and small intestinal segments. Such variability has resulted clearly also from the other studies and it was dependent on the animal species, site of occurrence (i.e. the gastrointestinal segment), and feeding conditions (Fleckenstein *et al.,* 1982; Romański, 2002; 2007).

In the present study, the MR was observed infrequently in the abomasal antrum. The pattern was seen there also in some other animal species (Fleckenstein *et al.,* 1982; Bortoff *et al.,* 1984). It was difficult to identify the antral MR after feeding. It is well known that feeding increases substantially the intensity of spiking activity what makes MR identification more difficult (Ruckebusch, 1970). The suggestion of Fleckenstein *et al.* (1982) that in sheep the antral MR does not migrate to the duodenum is, however, inconsistent with the presented and previous results since almost all of MR patterns migrated to the duodenum (see also Romański, 2002; 2003). In the obtained recordings, the MR was slightly less frequently observed in the upper jejunum. This confirms the observations of Fleckenstein *et al.* (1982) made in some animal species including sheep. In the jejunum, the MR usually differed from that in the duodenum. It contained usually more than 1–2 spike burst in one MR episode, what decreased its clarity and possibility of identification, especially when the surrounding spiking activity was more in-

tense. In the distal part of the jejunum, this was even more distinct. As it was frequently seen, the MR was virtually absent in these regions of the gut what was observed not only in the current, but also in previous studies (Romański, 2002; 2004).

The prevailing number of MR episodes was coordinated with the MR present, at least, in two adjacent sites examined herein. The electrode distances between the antrum and the duodenal bulb and even the duodenum in the applied model were rather not long. This could explain, at least in part, the high percent of coordinated MR patterns in the upper regions examined. The distance between duodenal and jejunal electrodes was longer, what could lower the percentage of coordinated MR observed in these sites. The presented results show the limited differences in the MR incidence and coordination before and after feeding. However, in ruminant animals, not exhibiting the interdigestive periods, the differences between the pre-feeding and post-feeding periods are not as marked as in monogastrics. The flow of digesta in both periods is almost constant in the ruminant species (Bueno *et al.,* 1975). Therefore, food cannot stimulate substantially the abomasum and the duodenum soon after feeding especially when the experiments conducted in non-fasted animals were compared. Consumed fodder may remain for relatively long time in forestomachs. This ruminant specificity may be a reason for the presence of the MMC pattern also after feeding as observed in sheep (Bueno *et al.,* 1975). The same may concern the MR in this species. The MR pattern is thus present in ruminants and also in monogastrics either during the interdigestive or the digestive state (Sarna & Otterson, 1989).

In the antroduodenum, the MR coordination was the highest. It can be partially linked with the arrival of the pyloric waves transporting the digesta to the duodenal bulb towards the distal duodenum (Gregory *et al.,* 1985; Fioramonti & Bueno, 1988; Houghton *et al.,* 1988; Lüdtke *et al.*, 1991). Efficient transport of acidified chyme through the gastroduodenal junction is desired to stimulate duodenal controlling mechanisms responsible for the intestinal phase of the gastroduodenal motility and secretion. These pyloric waves and sometimes also the giant spike bursts observed in the duodenal bulb may resemble the peristaltic (or retroperistaltic) rush (Meltzer & Auer, 1907). It is possible that they may contribute to the MR or replace it. In the duodenum, the arrival of the irregular and perhaps less propulsive fed pattern allows the digestive processes to continue (Gill *et al.,* 1985; Riachi *et al.,* 1996; Simonian *et al.,* 2005; Romański, 2008). The MR can rather be propulsive, migrating usually over the short distance in the gut (Sarna & Otterson, 1989). Sometimes the pattern exhibits the stationary nature. These MR features were also observed in the present study.

The propagation velocity of the MR observed here was not different from that seen in the previous study, i.e. reaching about 20 cm/s (Romański, 2002) or reported by others (Fleckenstein *et al.*, 1982). However, it can be so slow as about 2 cm/s that was observed either in this study or by others (Kellow *et al.*, 1986), similar to the migration speed of the slow waves in ovine antral region (Bueno & Fioramonti, 1980) or of peristaltic rush in the small bowel of man (Fleckenstein, 1978). In the jejunum, slow wave propagation velocity can be faster in sheep (Bueno & Fioramonti, 1980), that coincide with the presented values regarding the MR. The great differences in the propagation velocity of the MR results from its high vari-

ability and therefore affects considerably the transport efficiency of the MR pattern.

It is concluded that the MR incidence, form, and coordination including the propagation velocity depend upon the feeding conditions, intensity of intestinal motility and the gastrointestinal segment.

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Correspondence:

Prof. dr hab. Krzysztof W. Romański
Department of Animal Physiology,
Faculty of Veterinary Medicine,
University of Environmental and
Life Sciences,
Norwida 31, 50-375 Wrocław, Poland,
phone: +48 71 3205422, fax: +48 71 3201567,
e-mail: k.w.romanski@gmail.com;
krzysztof.romanski@up.wroc.pl