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Research Article

Occurrence and characteristics of the migrating myoelectric complex in ovine gallbladder and its relationships to the small intestinal motility

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ABSTRACT

An attempt has been made to identify the migrating motility complex in the ovine gallbladder and to span it with the small-intestinal pattern. For this purpose, four rams underwent surgical implantation of bipolar electrodes into the abomasal antrum, entire small bowel and gallbladder infundibulum, corpus and fundus. The strain gauge force transducer was also mounted in the gallbladder fundus, near the electrode. In the course of chronic experiments, the myoelectrical and motor activity was recorded in fasted and non-fasted rams, with or without feeding. Cyclic myoelectrical and motor activity pattern was found in the gallbladder. It resembled the migrating myoelectric complex present in the small bowel. The gallbladder pattern was well correlated with the intestinal migrating complex. Three or four phases of this pattern could be identified in all gallbladder regions. The most characteristic phase 3-like activity was longer and more intense in the gallbladder fundus as compared with the upper gallbladder regions. In both the small bowel and gallbladder, motility alterations caused by various feeding conditions were comparable. Therefore, the migrating motility complex occurs in the ovine gallbladder, albeit its putative role can be different from that in the small bowel, at least in part.

Keywords: Sheep; Gallbladder; Myoelectrical activity; Mechanical activity; Migrating motility complex.

1. INTRODUCTION

The principal roles of the gallbladder are to store and concentrate bile and to deliver it periodically towards the duodenum [1, 2]. Thus it exhibits the composed motor function. Permanent gallbladder filling and emptying facilitates normal enterohepatic circulation of bile acids [3]. The gallbladder exhibits phasic and tonic contractions being the strongest after feeding and evacuating almost all the gallbladder bile into the duodenum. In monogastrics, during the interdigestive period, gallbladder motility is also intense, particularly when phase 2 or phase 3 of the migrating motility complex (MMC) arrives in the small bowel. Therefore, cyclic gallbladder motor activity and cyclic bile evacuation into the duodenum occurs during this period [4]. In sheep, the presence of phasic and tonic gallbladder contractions has also been reported, except during short quiescent periods

in the course of phase 1 of the duodenal MMC cycles [5]. Feeding enhanced gallbladder contractility also in this species [6]. In scanty studies on sheep, cyclic character of gallbladder myoelectrical activity, few differences between the gallbladder neck and fundus and presence of the 'minute rhythm' were demonstrated as well [7, 8]. When the 'minute rhythm' occurs regularly in the ovine gallbladder, as in the upper small bowel, the presence of the MMC could also be expected, like in the proximal small bowel, as suggested in the dog [9] and in brief report in sheep [10]. Thus, the aim of this study was to identify and characterize the MMC in ovine gallbladder and to span it with the duodenal MMC.

2. MATERIALS AND METHODS

2.1. Experimental animals

Four adult rams of Polish Merino breed, each weighing 42 kg (range 39-43 kg), were used. Animals were clinically healthy and were not used previously for other types of the experiments. Before the surgery, they were kept in the spacious, clean and dry cages in small groups at the natural daily light rhythm. They were fed with a good quality hay and grain mixture (CJ mixture for calves and lambs, Dolpasz, Wrocław, Poland) according to the appropriate daily intake. Drinking water was not limited except in the course of the experiments.

2.2. Animal preparation

The bipolar platinum serosal electrodes and strain gauge force transducers were used for the recording of electrical and mechanical activity. The strain gauge force transducers (RB Products, Madison, WI, USA) were calibrated before implantation. In 24 h fasted rams, after 10-12 cm laparotomy, each animal was fitted with ten electrodes and one strain gauge force transducer under general and local anesthesia [11].

The electrodes were located as follows:

1 - the abomasal antrum, 4 cm proximally to the mid of the pyloric ring;

2 - the duodenal bulb, 6 cm distally to the mid of the pyloric ring;

3 - the duodenum, 50 cm distally to the bulbar electrode;

4 - the jejunum 1, 200 cm distally to the duodenal electrode;

5 - the jejunum 2, spaced 100 cm distally from the jejunal 1 electrode;

6 - the ileum 1, located 110 cm proximally to its termination, i.e. before the ileocecal junction;

7 - the ileum 2, located 10 cm proximally to the ileocecal junction;

8 - gallbladder infundibulum, 1 cm distally to the gallbladder neck;

9 - gallbladder corpus, 4 cm distally to the upper gallbladder electrode;

10 - gallbladder fundus, 4 cm distally to the mid of gallbladder electrodes.

The strain gauge force transducer was attached near gallbladder fundic electrode. After the surgery, animals were kept in single cages and feeding was gradually started from the second postsurgical day. Further details of the experimental protocol are available elsewhere [11, 12].

2.3. Experimental design

The total of 32 randomized experiments were conducted. Chronic experiments, lasting 6-8 h each, were started at least ten days following the surgery.

Four types of the experiments were carried out: [a] in 48 h fasted rams without feeding (control group), [b] in 48 h fasted rams with feeding during phase 2b of duodenal MMC (250 g of the grain mixture), [c] in non-fasted rams without feeding, [d] in non-fasted rams with feeding during phase 2b of the MMC identified in the duodenum (250 g of the grain mixture). Each type of the experiment was preformed twice: with or without mechanical activity recording (the myoelectrical activity recorded with ten electrodes). The mechanical activity was thus recorded from the fundic strain gauge force transducer replacing the ileal 2 electrode and the myoelectrical activity was recorded simultaneously from nine remaining electrodes. The data were derived from these experiments. The fodder was removed from the cage 1-2 h before each experiment performed in non-fasted rams. The myoelectrical and mechanical activity was recorded throughout the experiments using the 10-channel electroencephalograph (Reega) equipped additionally with the Wheatstone bridge for the recordings

of mechanical activity. After the initial period, lasting 15-40 min, at least two full small intestinal MMC cycles were recorded and then the recording was continued until the arrival of phase 2 of the subsequent MMC cycle.

2.4. Myoelectrical and mechanical recordings

Typical spike bursts along with the myo-electrical patterns were recorded in the abomasal antrum and entire small bowel. The phasic contractions and their myoelectrical correlates were principally recorded in the gallbladder fundus while in the remaining gallbladder regions, mostly the short spike bursts as the myoelectrical correlates of phasic contractions, were identified on the recordings. These events were principally organized in the cycles closely resembling the small-intestinal MMCs and were observed most clearly in the myoelectrical recordings. The subsequent MMC phase-like activity, i.e. the phases 1-3, were identi-fied in the gallbladder as well. Phase 4 was not always observed. Several parameters characterizing the duodenal and gallbladder MMC were calculated from the tracings: the MMC cycle duration, duration of the MMC phase, expressed both in minutes and in percentage of total cycle duration, coordination of the gallbladder phase 3 of the MMC with those in the duodenum, the propagation (migration) velocity of phase 3, the amplitude and duration of the phase 3-spike bursts and the contractions forming phase 3 of the MMC. The propagation velocity of phase 3 of the MMC was expressed as the overall parameter (for the whole gallbladder). Additionally, its posi-tive values (aboral migration) and negative values (oral migration also called the retropropagated event) were presented separately. The representative figures illustrating the gallbladder MMC were also shown.

2.5. Statistical data elaboration

The mean values and standard deviations were calculated where appropriate. Then, the Student *t*-test for paired values, preceded by analysis of variance, was used [13]. Statistical significances ($P<0.05$, $P<0.01$ and $P<0.001$) were introduced into the tables.

2.6. Ethical approval

Protocol of the study and informed consent were in compliance with the Helsinki convention and were approved by local Ethics Committee.

3. RESULTS

In the recordings of electrical activity, the myoelectric correlates of phasic contractions (short-lasting spike bursts of various duration, lasting usually 0.2-1.5 s) were observed in all the regions examined. Mechanical recordings divulged the presence of both phasic and tonic contractions in the gallbladder fundus. The MMC was conclusively identified in the entire small bowel and gallbladder in all the experiments performed. In the abomasal antrum, the MMC was absent and in the duodenal bulb it was usually greatly reduced. Duration of the MMC cycle in the small bowel was very similar to that in the gallbladder regardless of feeding conditions (Table 1). It was longer after feeding, but changes were not statistically significant. The MMC phases 1-4 were identified both in the small bowel and the gallbladder (Fig. 1, 2). Duration of phase 1 of the MMC in the gallbladder was similar in the various gallbladder regions regardless of feeding conditions (Table 1). Duration of phase 2 of the MMC was significantly longer after feeding than in not fed rams. Similar difference was observed between fasted and non-fasted rams. Duration of phase 3 of the MMC was significantly longer in the gallbladder fundus than in the infundibulum and corpus (Table 1, see also Figs. 1, 2). After feeding, duration of phase 3 in the gallbladder fundus was significantly shorter than in not fed animals. Phase 4 of the MMC was often present, but in few cases it was virtually absent. Phase 4, despite its variable duration, was significantly longer in the gallbladder corpus after feeding than in not fed animals (Table 1). Phase 3 of the MMC in the gallbladder was well coordinated with that in the duodenum (Table 2, Fig. 3). However, coordination of phase 3 of the MMC in the gallbladder infundibulum and corpus with duodenal phase 3 was different. Sometimes the onset of phase 3 in the gallbladder preceded the onset of phase 3 in the duodenum. In other cases, it was slightly delayed.

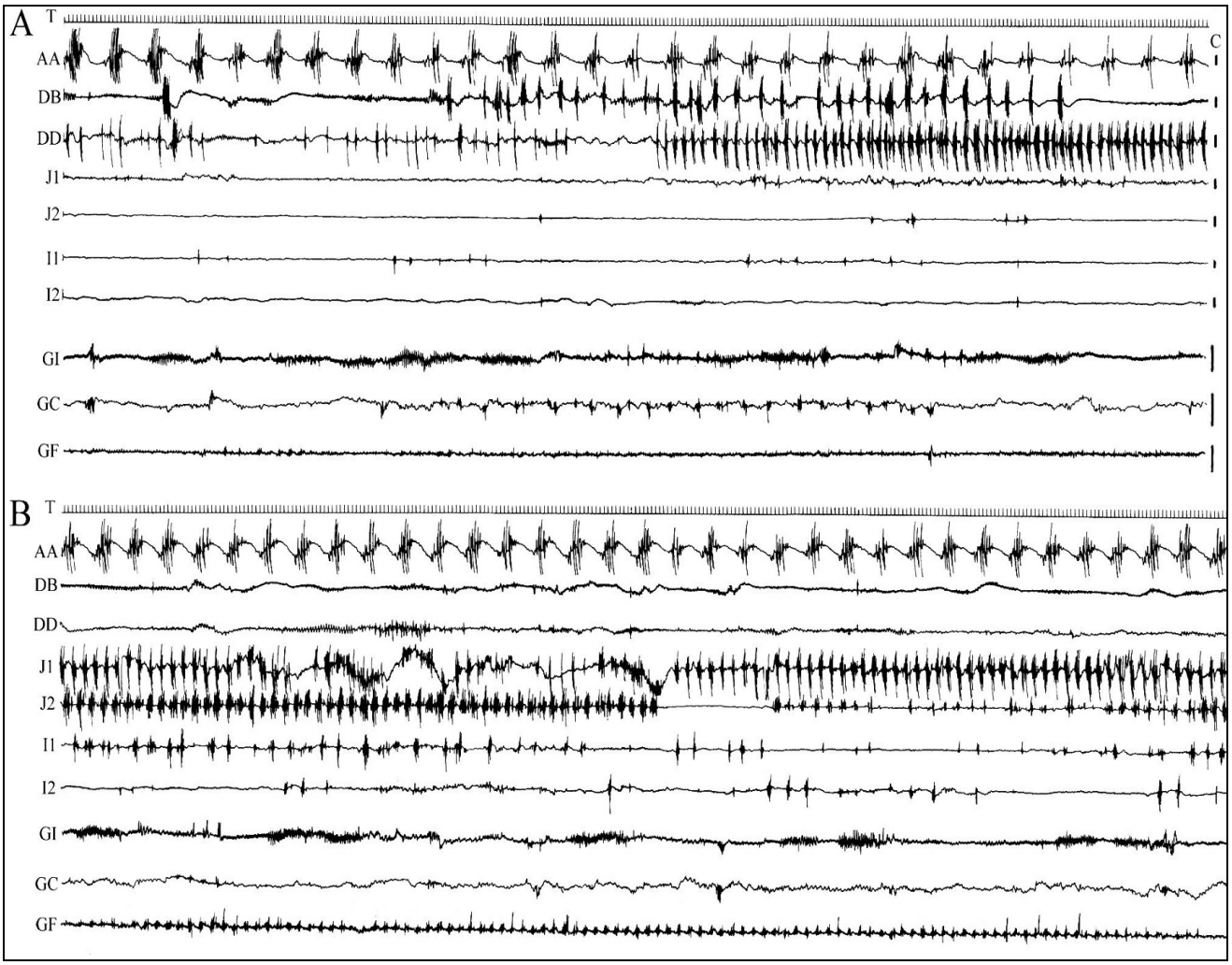

Figure 1. The presence of the migrating motility complex (MMC) in small intestine and the gallbladder of non-fasted ram. Two five-minute electromyographical recording fragments separated with 2.5 min. brake are shown.
Panel A: Phase 3 in the duodenal bulb (shortened) and phase 3 of the MMC present at the same time in the gallbladder infundibulum slightly preceded by phase 3 in the gallbladder corpus. In the gallbladder fundus, phase 2 of the MMC is noticeable. In the gallbladder infundibulum, the short-lasting spike bursts are alternated with the long-lasting spike bursts. Note that phase 3 in the abomasal antrum cannot be identified because of the continuous maximal spike bursts.
Panel B: Phase 3 is present in the jejunum and in the gallbladder fundus where it is followed by very short phase 4 of the MMC. In the gallbladder infundibulum and corpus, phase 1 of the MMC is visible.
Explanations of symbols: T, time in seconds. Electrodes: AA, abomasal antrum; DB, duodenal bulb; DD, duodenum; J1, jejunum 1; J2, jejunum 2; I1, ileum 1; I2, ileum 2; GI, gallbladder infundibulum; GC, gallbladder corpus; GF, gallbladder fundus. C, calibration, 100 μV. Other explanations as in the section Materials and methods.

In the gallbladder fundus, phase 3 of the MMC arrived few minutes later than in the upper gallbladder (Table 2). The propagation velocity of phase 3 of the MMC, observed in the gallbladder, differed substantially. While measured between gallbladder infundibulum and corpus, the values were sometimes negative due to retropropagation of phase 3 in the upper gallbladder region. Therefore, the overall values were fairly dispersed since they contained both positive and negative values. Furthermore, no marked differences related to feeding conditions were denoted in the gallbladder, except markedly and significantly lower negative values in not fed animals, studied either with or without feeding, as compared with the fasted animals (Table 2). In the lower gallbladder region, i.e. when the propagation velocity was measured between gallbladder corpus and fundus, the values were much lower than the values obtained from the upper gallbladder region (Table 2).

Table 1. Characteristics of the migrating motility complex-like activity in the ovine gallbladder in various feeding conditions.

			MMC cycle duration (min)		Duration of gallbladder MMC phases (min)											
					Phase 1			Phase 2			Phase 3			Phase 4		
			duod.	gallbl.	infund.	corpus	fund.	infund.	corpus	fund.	infund.	corpus	fund.	infund.	corpus	fund.
Fasted	not fed	n=	4	4	4	4	4	4	4	4	4	4	4	3	3	2
		mean	61.3	61.8	19.8	19.8	18.3	39.8	40.3	38.3	1.9	1.6	5.3^{z}	0.4	0.3	0.5
		±S.D.	25.4	25.1	6.7	9.1	8.0	18.1	16.7	18.5	0.5	0.9	0.7	0.2	0.2	0.3
		%	-	100.0	32.0	32.0	29.6	64.4	65.2	61.9	3.0	2.6	8.5	0.6	0.5	0.8
	fed	n=	4	4	4	4	4	4	4	4	4	4	4	4	4	4
		mean	94.3	94.3	21.8	20.8	19.0	70.0^{a}	69.3^{a}	70.3^{a}	1.5	1.9	3.9^{az}	1.0	1.5^{a}	1.0
		±S.D.	17.0	18.1	8.7	7.9	7.6	13.1	13.9	13.8	0.5	1.1	0.7	0.5	0.9	0.7
		%	-	100.0	23.1	22.0	20.2	74.3	74.0	74.5	1.6	2.0	4.1	1.0	1.6	1.0
Not fasted	not fed	n=	4	4	4	4	4	4	4	4	4	4	4	4	2	3
		mean	80.0	79.5	24.5	25.3	20.8	53.0	52.0	53.5	1.8	1.8	4.7^{z}	0.4	0.5	0.6
		±S.D.	22.7	24.0	7.7	8.8	10.9	15.9	17.8	14.2	0.4	0.4	0.9	0.3	0.1	0.5
		%	-	100.0	30.8	31.8	26.1	66.7	65.4	67.3	2.2	2.2	5.9	0.4	0.6	0.8
	fed	n=	4	4	4	4	4	4	4	4	4	4	4	4	4	4
		mean	100.3	100.5	26.0	26.0	26.3	72.0^{a}	72.0^{a}	69.5^{a}	1.6	1.5	4.0^{az}	0.9	1.2^{b}	0.8
		±S.D.	19.1	19.2	7.5	7.6	5.1	11.5	12.8	14.0	0.3	0.7	0.6	0.6	0.5	0.5
		%	-	100.0	25.9	25.9	26.1	71.6	71.6	69.2	1.6	1.5	4.0	0.9	1.1	0.8

Explanations: %, percent of the total MMC cycle duration, ^{a}, P<0.05; ^{b}, P<0.01 vs. relevant value in fasted animals, ^{z}, P<0.001 vs. relevant value in gallbladder indundibulum. Other explanations as in the section Materials and methods.

Table 2. Characteristics of phase 3 of the migrating motility complex-like activity in the ovine gallbladder in various feeding conditions.

			Duodenum-gallbladder phase 3 coordination (min)			Propagation velocity of gallbladder phase 3 (cm/min)				Spike burst amplitude of gallbladder phase 3 (μV)			Contract. amplit. (g)	Spike burst duration of gallbladder phase 3 (s)			Contract. duration (g)
			infund.	corpus	fund.	infundib.-corpus *total*	infundib.-corpus *posit.*	infundib.-corpus *negat.*	corp.-fund. *(posit.)*	infund.	corpus	fund.	fundus	infund.	corpus	fund.	fundus
Fasted	not fed	n=	4	4	4	4	1	3	4	4	4	4	4	4	4	4	4
		mean	0.5	-0.15	5.0	22.7	5.0	28.6	0.8	55.3	55.3	55.0	2.1	1.3	1.2	1.1	5.1
		±S.D.	0.8	0.4	2.2	20.0	0.0	18.1	0.5	7.1	7.5	8.8	0.3	0.4	0.2	0.4	0.4
	fed	n=	4	4	4	4	3	1	4	4	4	4	4	4	4	4	4
		mean	0.0	0.8	9.0	15.7	7.5	40.0	0.6	30.8^{c}	28.0^{c}	28.5^{c}	1.5^{a}	1.6	1.6	1.5	4.2^{a}
		±S.D.	0.4	0.3	4.0	16.8	5.1	0.0	0.3	8.2	8.3	6.1	0.3	0.3	0.2	0.3	0.3
Not fasted	not fed	n=	4	4	4	4	2	2	4	4	4	4	4	4	4	4	4
		mean	-0.7	-1.0	5.3	6.5	8.5	4.5^{b}	1.0	41.8	39.0^{a}	41.0	1.6^{a}	1.1	1.1	1.1	4.7
		±S.D.	-0.4	0.7	1.9	2.6	2.1	0.7	0.4	9.5	10.7	10.6	0.2	0.3	0.6	0.4	0.3
	fed	n=	4	4	4	4	3	1	4	4	4	4	4	4	4	4	4
		mean	0.1	0.8	9.3	2.7	2.9	2.3^{c}	0.8^{a}	37.8^{c}	38.0^{b}	36.5^{b}	1.2^{b}	1.0	0.9	1.0	3.8^{b}
		±S.D.	0.4	1.5	5.8	0.9	1.0	0.0	0.6	5.1	5.2	4.0	0.2	0.4	0.3	0.3	0.2

Explanations: *posit.*, positive values only (phase 3 propagated); *negat.*, negative values only (phase 3 retropropagated) ^{a}, P<0.05; ^{b}, P<0.01, ^{c}, P<0.001 vs. relevant value in fasted animals. Other explanations in the section Materials and methods.

The amplitude of the spike bursts of phase 3 of the MMC observed in all the gallbladder regions, was significantly lowered after feeding when compared with fasted animals. In the non-fasted, not fed rams, the lowering tendency of this parameter in the gallbladder infundibulum and fundus was observed, while in the gallbladder corpus it achieved the level of statistical significance when compared with fasted rams (Table 2). The amplitude of phase 3 contractions in the gallbladder fundus was

significantly higher in fasted - not fed animals as compared with other experimental groups (Table 2). Duration of the spike bursts forming phase 3 of the gallbladder MMC was higher in fasted animals after feeding than in the control group and than in non-fasted rams (Table 2).

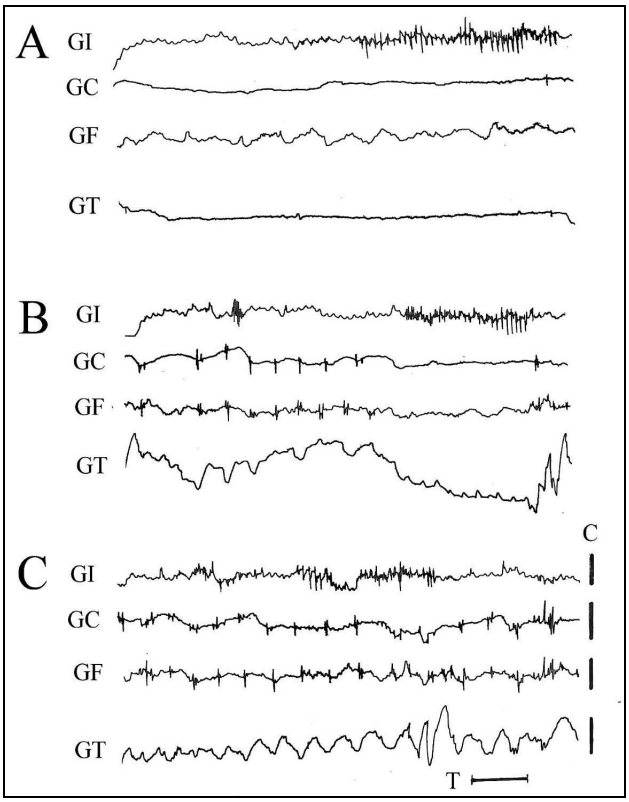

Figure 2. The subsequent phases of the migrating motility complex (MMC) in the gallbladder of non-fasted ram, recorded during the same MMC cycle. Note the presence of the long-lasting spike bursts in the gallbladder infundibulum during all the MMC phases.
Panel A, phase 1 of the MMC. Panel B, phase 2 of the MMC. Panel C, phase 3 of the MMC.
Explanations of symbols: GT, strain gauge force transduced in gallbladder fundus. C, calibration, 100 μV. T - time, 10 s, 2.5 g. Other explanations as in the legend to Fig. 1.

Duration of phase 3-related contractions in the gallbladder fundus was shortened in both groups studied with feeding procedure when compared with the relevant data obtained from the experiments performed in fasted animals (Table 2). Fig. 4 presents the fragments of well-developed phase 3 of the MMC in the gallbladder fundus of fasted rams. In the gallbladder infundibulum and also frequently in the gallbladder corpus, the so-called long-lasting spike bursts were observed during all the MMC phases (see Fig. 1).

In the course of additional experiments the recordings were similar to those obtained from proper experiments and phase 3 of the MMC was also observed in all recording channels, except the abomasal antrum, including the recordings from the ileal 2 electrode.

4. DISCUSSION

The MMC cycles were observed both in the small bowel and gallbladder in all the experiments performed. The MMC pattern in the ovine gallbladder was more evident in the electromyographical than in mechanical recordings because of the character of gallbladder motor function. Analysis of the mechanical recordings showed that short-lasting contractions were often combined with the relatively frequent long-lasting contractions and made the analysis of the short-lasting (phasic) contractions unclear. There are several similarities between gallbladder motility in sheep [7, 8, 14, 15] and in monogastric species [16-19] comprising its complexity, relations to the interdigestive motility of the small bowel and character of gallbladder emptying. The long-lasting contractions including giant cotractions are known to be present both in the gallbladder and the gut [20-22]. Tonic contractions are also present both in the small bowel and gallbladder although no their myoelectric correlates have been described. In the gallbladder, tonic contractions occur mostly after feeding as the slow, smooth contractions that are responsible for gallbladder emptying [1]. Phasic contractions are often super-imposed on tonic contractions [17]. Since no myoelectric correlates of tonic contractions were observed in the gallbladder, the MMC was more evident in the myoelectrical recordings than in the mechanical recordings. Its wall is relatively thin and it is not easy to obtain the good quality myoelectrical recordings. Since in the earlier report Ludwick and Bass [23] did not find the electrical activity in the gallbladder of the dog and monkey, technical difficulties were probably the reason. This is improbable because the muscle layer is present in the gallbladder and Matsumoto et al. [24] obtained positive results in the dog.

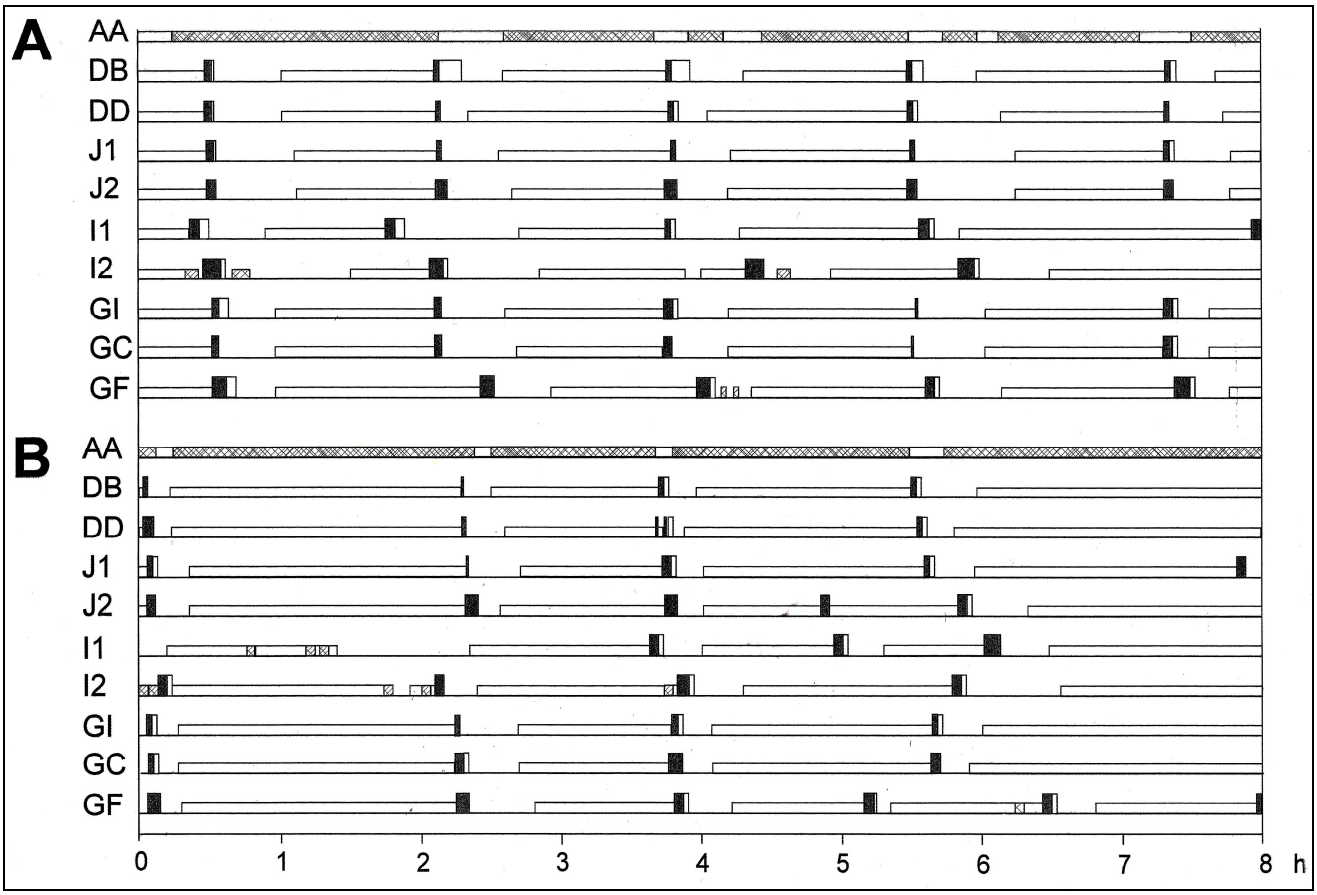

Figure 3. Scheme of the gastrointestinal and gallbladder migrating motility complex (MMC) based upon the eight-hour myoelectrical recordings. Upper panel, fasted rams; lower panel, not fasted rams; scheme of the experiments performed in the same animal.

Bars: crossed bars, maximal myoelectric activity observed in the abomasal antrum, ileum and gallbladder fundus, not interpreted as phase 3 of the MMC; open low bars, phase 2 of the MMC; closed high bars, phase 3 of the MMC, open high bars, phase 4 of the MMC; no bar, phase 1 of the MMC. Other explanations as in the legend to Fig. 1.

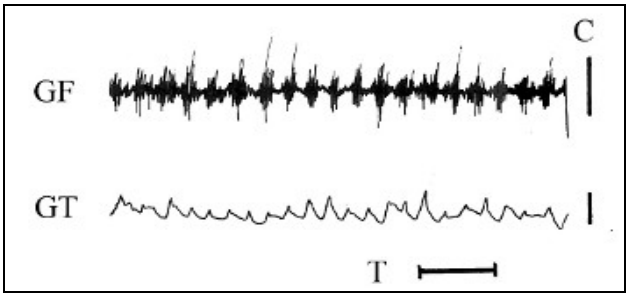

Figure 4. Fragments of phase 3 of the migrating motility complex in gallbladder fundus of fasted ram.

Explanations: GF, the myoelectrical activity recording from gallbladder fundus; GT, motor activity recording from gallbladder fundus. C, calibration, 50 μV and 2.5 g, T, time, 10 s.

Only few full reports clearly presenting the gallbladder myoelectrical activity are available in sheep [7, 8, 11, 15] and in pigs [25]. None of them described the MMC in the gallbladder. The studies utilizing the mechanical recording methods of gallbladder motility examination demonstrated periodic alterations of gallbladder motor function in concert with the duodenal MMC, but not visualized the MMC there [16, 17]. There were, however, few suggestions that the MMC is present in the gallbladder [9, 10].

This report presents the evidence and further confirmation that the MMC occurs in animal gallbladder. Although the MMC demonstration appeared clear enough, marked regional differences may accomplish the interpretation of the gallbladder myoelectrical and motor recordings. The coordination of phase 3 of the MMC between the upper (gallbladder infundibulum and corpus) and lower part of the organ (gallbladder fundus) is different than the coordination between the gallbladder

infundibulum and gallbladder corpus. Thus in the gallbladder, the 'cleaved phase 3' of the MMC is present. The apparent role of shorter propagated phase 3 of the MMC in the gallbladder infundibulum, and also in the gallbladder corpus, is to facilitate the gallbladder bile inflow and perhaps also mixing of bile. Sometimes the direction of propagation of phase 3 in the upper gallbladder can be reversed (retropropagated phase 3) which, along with tonic contractions, may promote gallbladder bile evacuation. In the gallbladder fundus, periodic arrival of the longer phase 3 of the MMC may guarantee good mixing and stirring of the gallbladder content preventing crystallization of biliary sediment. Its role in bile transport seems doubtful. The mixing in the gallbladder fundus appears more important than in its proximal parts.

Furthermore, in the ruminants, more continuous than that in monogastrics, evacuation of the bile into the duodenum is probable since in these species rather uninterrupted digestive processes occur in the intestinal lumen. Therefore, intense gallbladder motility represents its specific character being easily adaptative to the situation in the bowel.

Longer myoelectrical events, observed mostly in the gallbladder infundibulum, but also in other gallbladder regions, resembled to some extent the long-lasting spike bursts described in the ovine colon [26]. They were not related to the MMC. Bueno and Praddaude [7] suggested the presence of clusters of spike potentials occurring at regular intervals in the ovine gallbladder. They could serve as the myoelectric correlates of long-lasting contractions and contribute to bile transport.

The role, character and functioning of ovine gallbladder motility does not appear to be much different from that in monogastric species including man [6, 14, 15, 27, 28]. The results obtained from the studies on ovine gallbladder motility can be similar to those in monogastrics and the question arises whether the ovine gallbladder motility model can serve as the relevant model for monogastrics.

By virtue of obtained results it can be concluded that the MMC occurs in ovine gallbladder and is correlated with the MMC pattern observed in the small bowel. Therefore, it can be expected that in other species the MMC in the gallbladder will also be described and this report makes the first base.

TRANSPARENCY DECLARATION

The author declares no conflicts of interest.

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