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Patterns of electrical activity in the digestive tract of the conscious cat

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1. Bipolar electrodes were permanently implanted on the gastric antrum, and on the different portions of the small intestine of each of eleven healthy adult cats receiving one meal daily. All parts of the feline gut exhibited, as in several other species, regular slow waves and alternate periods of quiescence and electrical spiking activity during the recording sessions lasting from 10 to 30 d.

2. Patterns of electrical activity characteristic of this species were identified. Both the amplitude and frequency of the antral slow-wave were related to the presence of superimposed spike bursts during fasting. A decrease in the antral slow-wave frequency and increase in the length of the duodenal plateau of slow waves after the daily meal were related to its nature.

3. In fasted state, the electrical spiking activity of the small intestine occurred as fused spike bursts of large amplitude potentials migrating slowly over short distances only 24 h after feeding. They are interspersed with short periods of irregular spiking activity.

4. These findings suggested that, except the distal part of the small intestine which showed an activity which resembled partially the migrating myoelectric complex observed in other species during the fasting state, the motility patterns of the digestive tract in the cat were not comparable to those observed in the dog or sheep. In the cat, mixing of the contents seemed to result from more or less regular spiking activity allowing their propulsion distally. The propagation over distances varying from 200 to 1000 mm of nine to eighteen daily fused spike bursts in the fasting state remains unclear but they are related to the digestive function in accordance with the displacement aborally of their origin in a prolonged fasting condition.

After the first description of migrating myoelectrical complexes (MMC) along the small intestine in the fasted dog (Szurszewski, 1969) numerous studies have both confirmed their presence as a basic pattern in many mammalian species except the cat (Grivel & Ruckebusch, 1972; Ruckebusch & Fioramonti, 1975) and defined their function in the transit of digesta (Bueno *et al.* 1975).

Absence of a patterned MMC in the cat was confirmed by Weisbrodt & Christensen (1972) who observed after a 24 h fasting period the propagation of long fused spike bursts lasting 1·5–2 min, starting on the duodenum as well as on the proximal jejunum. In contrast with their results, Weinbeck *et al.* (1972) showed phases of regular spiking activity with similar characteristics to the regular spiking activity (RSA) of MMC on the ileum near the ileocaecal junction.

On the basis of these results, the two objectives of these experiments were to define the patterns of electrical activity of the muscular layers of the gastrointestinal tract in relation to feeding behaviour and to determine the nature and origin of these long fused spike bursts.

MATERIALS AND METHODS

Animal preparation

Eleven adult cats weighing approximately 2·5 kg and receiving a daily meal of either 60 g canned food or 60 g beef liver were used for these investigations. Under general anaesthesia with pentobarbital (Nembutal, 30 mg/kg, Abbott) twelve pairs of electrodes made of insulated nichrome wires, 80 μm in diameter and 1000 mm in length were fixed 2 mm apart into the muscular layers of the antrum and duodenum at respectively 5, 10, 15, 20 mm before the pylorus and 10 mm and 50 mm after the pylorus, on the jejunum at 400, 800, 1000 mm from the Treitz ligament. Two additional groups were placed on the ileum at 250 and 50 mm from the ileo–colonic junction. The electrodes were exteriorized in the dorso-scapular region, fixed to the skin in a small leather bag secured by cords around the thorax.

Electrical measurements

The animals were placed in wooden cages with a large glass panel on one side and the electrodes were connected to an electroencephalograph (Reega XII, Alvar, Paris) using a rotative multi-channel connector. Direct recording of electrical activity started 15 d after surgery and was performed continuously over a period of 2 months, at a time constant of 0·5 s. The spiking activity of four groups of electrodes was continuously summed at 20 s intervals and automatically plotted by means of a linear integrator connected to a potentiometric recorder. Values of the basic electrical rhythm (BER) and velocity of propagation of the spike bursts were determined by inspection of the direct EMG record. Statistical analyses of the change of BEr after feeding (beef liver, canned food or milk) were performed from the mean value obtained over 30 min periods (before and after feeding) using the paired *t* test.

Experimental procedure and diet

During the preliminary 7 d control period the animals received a daily meal of 60 g canned food (Fido) or beef liver at 9.30 hours with water *ad lib.* Animals returned to the control diet after a 5 d fast and a period during which they received in three consecutive days either 50 g milk or fresh meat offered in one daily meal. Then the animals were killed with a lethal dose of pentobarbital (50 mg/kg).

RESULTS

Basic motility patterns

The pattern of electrical activity recorded from the antrum and the small intestine during the interdigestive phase, i.e. from 18 to 24 h after the last meal, showed the following characteristics. On the antrum, rhythmic slow wave potentials originated at 50–60 mm before the pylorus and recurred at a frequency of $4·8 \pm 0·4$ cycles/min; they were propagated aborally to the pylorus with a mean velocity of 45 ± 2 mm/min. However, this BER presented arrhythmias in relation to spiking activity, the lengthening of the BER occurring just after a propagated burst of spikes (Fig. 1). These bursts of spike potentials appeared cyclically superimposed on one or two consecutive antral slow waves at 1·2–1·5 min intervals giving a pattern of activity occupying approximately 30% of the recording time.

On the small intestine, values for BER were similar to those obtained for other species of carnivores (duodenum $18·9 \pm 0·4$ cycles/min, ileum $12·1 \pm 0·3$ cycles/min). They decreased along the small intestine after a plateau, the length of which was highly characteristic of the individual animal. The duodeno–jejunal length upon which this plateau was observed varied from 200 to 750 mm (Fig. 2). In animals regularly fed, spiking activity of the duodenum and jejunum was only irregular (ISA) similar to the ISA of MMC observed in

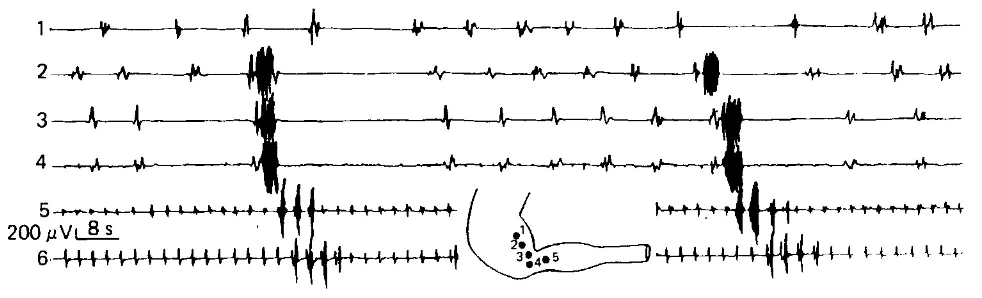

Fig. 1. Typical records of electrical activity of the gastrointestinal tract in cat during interdigestive state. The antral slow wave frequency presents arrhythmias associated with the cyclic occurrence of spike bursts passing through the gastroduodenal junction. Each burst is preceded by an increase in the gastric basic electrical rhythm and followed by a 20 s quiescent phase without antral slow wave.

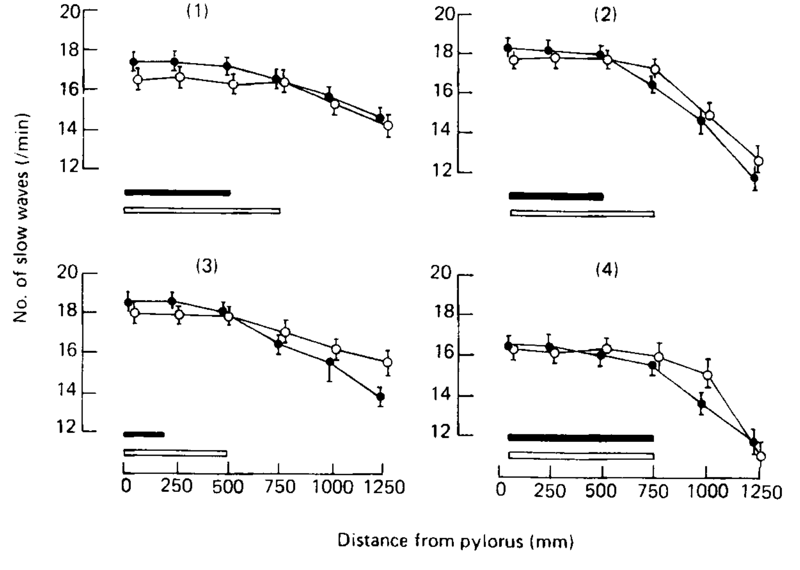

Fig. 2. Length of the duodenal plateau (▬, ▭) in each of four cats, fed or fasted. Except for cat no. 4 for which the plateau of 750 mm remained unchanged in the fasting state, the length was reduced during fasting by 30 and 50% respectively for cats nos. 1 and 2 (▬), fasting from 12 h; (▭), 1–3 h after feeding.

other species, with some short periods of reinforced spiking bursts interspersed with quiescent phases. The last peculiarity of the interdigestive pattern was the presence on ileum of long phases of RSA which can be propagated either in orthodromic or in antidromic direction over a 200–300 mm segment.

Fasting pattern

The main characteristic of antral activity was the regular occurring of arrhythmias of the BER, its mean value not being significantly ($P < 0{\cdot}05$) different from that observed 2 h before feeding. These arrhythmias only occurred within 15 s before or after a burst of spikes. More than 24 h after the last meal, spiking activity of the antrum appeared, as in the interdigestive state, cyclically superimposed to the slow waves in two or four consecutive

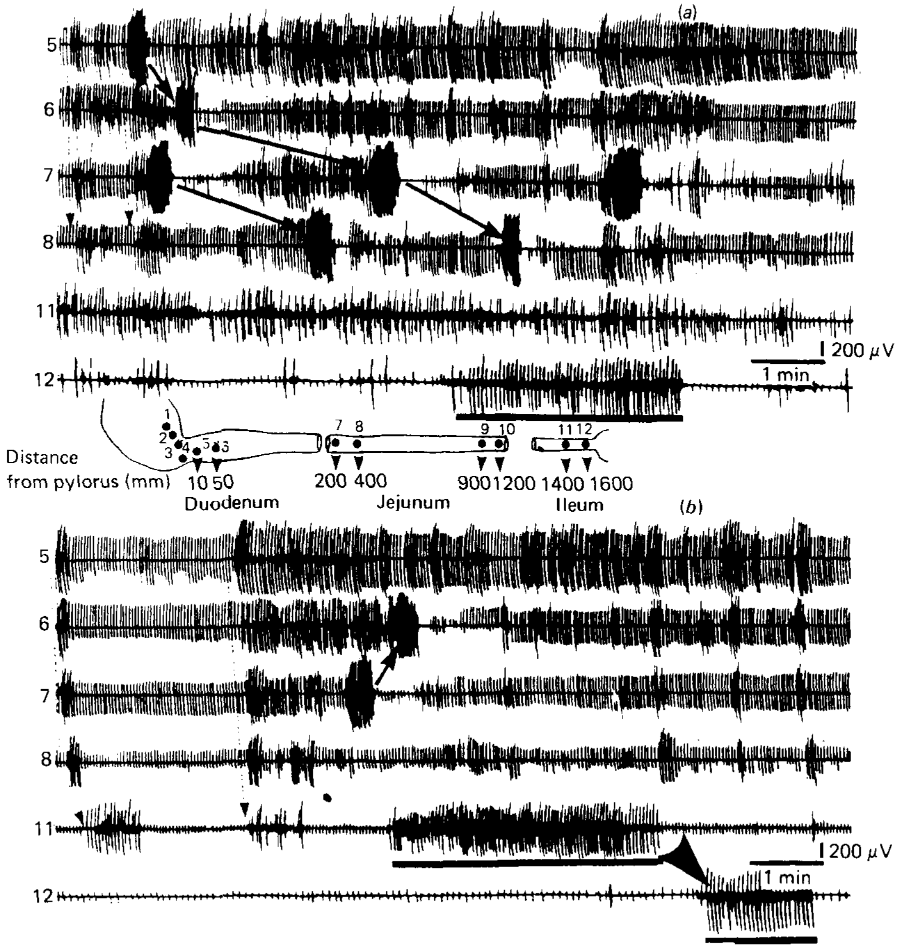

Fig. 3. Patterns of electrical activity of the small intestine in the fasted cat. (a) Isolated or serial migrating fused spike bursts are propagated aborally (→) along the duodenum and jejunum at a velocity of 30 mm/min after a 48 h fast. (b) After a more drastic fast (96 h) they can be propagated orally. In the ileum, migrating fused spike bursts (MFSB) are absent and the migrant myoelectric complex present. MFSB are followed by a short quiescent phase. (--→), the cyclic propagation of irregular spiking activity. (▬), The phases of regular spiking activity in the ileum; (▶), their propagation.

bursts occurring at 1·5–2 min, similar to the minute rhythm described in pig or dog. In prolonged fasting conditions, the intestine spiking activity presented the irregular spiking activity described in normal state and migrating fused spike bursts (MFSB) lasting approximately 10 s–2 min with high voltage (400–800 μV) occurring six to eighteen times/24 h (Fig. 3). Occasionally they were propagated along the whole intestine, but in most of the instances, they started on the duodenum or the proximal jejunum. As shown in Table 1, during the first 2 d of fasting the majority of MFSB originated from the upper part of the small intestine: ten daily MFSB in place of 2–3 for the lower part of the small intestine. This value was progressively reversed and 3–4 d later only nine ($\pm$4) daily MFSB were observed on the proximal duodenum *v.* seventeen ($\pm$6) at 1000 mm from the pylorus. The MFSB propagated only aborally or, after at least a 72 h fasting, orally (20%) along distances varying from 200 to 650 mm.

Table 1. *Effects of fasting on the frequency and origin of the migrating fused spike bursts (MFSB) in the cat*

(Mean values and standard deviations for thirty-three determinations in eleven cats between six and nine weeks after surgery. More MFSB were recorded in the proximal intestine at the beginning of fast, then after a 2 d fast)

	Distance from pylorus (mm)									
	50		200		900		1100		1400	
Day of fast	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	1	2	—	—	—	—	—	—	—	—
2	15	3	7	3	11	4	2	2	2	3
3	16	4	7	3	10	4	13	4	9	3
4	9	4	8	2	11	3	15	3	17	6

Table 2. *Effect of feeding on the antral basic electrical rhythm (cycles/min) in cat*

(Mean values for twelve meals of 60 g beef liver, 60 g canned food or 50 g milk for eight cats)

Meal	Food intake (g)	Control period		Feeding period		10–15 min after feeding		25–30 min after feeding	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Beef liver	60	4·9	0·4	5·5	0·3*	5·9	0·1**	5·7	0·2**
Canned food	60	5·3	0·7	4·6	0·7NS	5·1	0·3NS	5·2	0·2NS
Milk	50	5·5	0·6	5·2	0·3*	7·2	0·2**	6·6	0·8**

NS, not significant. Mean values were significantly different from control values at $^*P \leqslant 0·5$, $^{**}P \leqslant 0·05$.

Each MFSB was followed by a transient absence of BER; the duration of these silent periods increased from the duodenum (0·4 min) to the terminal part of the jejunum (0·8 min) in relation to the duration of the MFSB. But at the distance of 300–400 mm from the ileo-colonic junction, the duration of MFSB did not exceed 20 s and then these bursts were absent on the final 100 mm of the ileum. In contrast, phases of regular spiking activity were present and propagated aborally or orally on the ileal distal segment. The presence of MFSB decreased after 3 d of fasting and disappeared after 5 d of fasting.

Post-prandial pattern

Feeding was always accompanied for a period of 8–12 h by the disappearance of arrhythmias of the gastric BER independently of the nature of the food constituents. After this primary effect of food intake, differential changes were related to food constituents (Table 2). When cats received a meal consisting of 60 g beef liver the mean antral slow wave frequency increased by 15–22% from 30 min to 2 h. In contrast, a significant change in the slow wave frequency occurred after ingestion of 60 g canned food. Similarly drinking milk (50 ml) increased the antral BER by 26% but only for 60–90 min. Feeding (canned food or liver) increased the mean level of spiking activity; spike bursts were superimposed on 76% of the antral slow waves from 0 to 15 min after feeding compared with 37% in the control period i.e. 15 min before food intake. In contrast to the antrum, the mean values of the BER in both the duodenum and the ileum, but not in the jejunum, were significantly ($P \leqslant 0{\cdot}01$) reduced by feeding and in addition the length of the duodenal plateau was increased by 43% compared to the interdigestive state. Canned food or beef liver intake was accompanied by an abrupt increase in the mean spiking level for the upper duodenum and, more generally, for the oral first-third of the small intestine. In all cats strong spike bursts were superimposed to 85 and 45% of the slow waves at 10 and 200 mm from the pylorus respectively. After feeding, the activity of the duodenum was maximum for approximately 90 min and then decreased progressively; for 12–16 h, this pattern included alternate 2–2·5 min quiescent periods interspersed with a short (25 s) spiking phase propagated on the intestine tract near to the jejuno–ileal junction. Autonomy of the ileum persisted in the various diets: the main change was a disorganization of the RSA for 2–3 h and then a progressive increase in their occurrence during the entire duodenal activation.

DISCUSSION

The cyclical changes in the slow wave frequency occurring during fasting may be considered as a minute rhythm activity since the lengthening of the slow wave intervals was associated with cyclic spike bursts previously described in the dog (Ormsbee & Mir, 1977), the pig (Rayner & Weekes, 1978) and humans (Fleckenstein, 1977). In the cat, the frequency of antral slow waves appears greatly influenced by feeding and by the nature of food whereas these factors are poorly involved in man (Wingate *et al.* 1976) and the dog (Bueno, 1979). These species differences and the influence of the nature of food may be related to release of gastrointestinal hormones such as gastrin. Gastrin infusions are known to suppress BER arrhythmias of the antrum and to increase its frequency (Bueno & Garcia-Villar, 1979). An additional study is in process to assess this hypothesis. A striking feature of the intestinal spiking organization in the cat is the absence of the MMC in the duodenum and the jejunum, and their presence in the terminal ileum, as they are in the entire intestine of all other domestic animals investigated such as the rat, dog, rabbit, guinea pig, sheep, goat, pig, cow and horse (Szurszewski, 1969; Grivel & Ruckebusch, 1972; Bueno *et al.* 1975, 1977). Another feature of the feline intestinal motility pattern is the presence of MFSB during fasting, particularly in the duodeno–jejunal area. This pattern, previously described by Weisbrodt & Christensen (1972) can be related to the observations of rapidly moving barium in radiographic studies. However the role of these MFSB is very obscure because they occur in fasted animals and during 2–4 d. Weisbrodt & Christensen (1972) considered these MFSB as a variant of the interdigestive migrating spike potentials complex seen in the fasted dog. But the MMC first observed in the fasted dog was observed in other species independently of the feeding behaviour and they have a major function in the propulsion of digesta (Bueno *et al.* 1975). In the fasted dog, each MMC propels small amounts of digestive secretions (approximately 20 ml/h). Under these conditions, the 6 min duration of RSA of the MMC does not seem necessary for this propelling function and can be considered as a housekeeper activity. One MFSB corresponding to a long contracted intestinal segment moving slowly is as efficient and may be considered as a functional adaptation in cats, but the problem of the conversion to the RSA phases on the distal ileum remains unclear as well as their neuro-hormonal control and the mechanism involved in their propagation.

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