The *Fusus coli* of the Rabbit as a Pacemaker Area

Y. Ruckebusch and J. Fioramonti

Laboratoire de Physiologie, Ecole Nationale Vétérinaire, 23, chemin des Capelles, F–31076 Toulouse Cédex (France), 18 February 1976.

Summary. Section of the rabbit's proximal colon orad to the *fusus coli* resulted in a marked reduction in both slow-wave frequency and differentiation of the two kinds of faeces produced. This indicates the existence of a pacemaker area and a mechanical role for the reversed oral-aboral gradient of the proximal colon.

The rabbit has a highly specialized mechanism, which not only retains digesta in the proximal colon and caecum for the time required for microbial digestion of cellulose, but also allows formation of soft and hard faeces. A mid-colonic pacemaker area initiating anti-peristaltic waves of contraction towards the caecum and peristaltic waves towards the rectum has been described to explain the physical separation of liquid and solid digesta in the rat and the guinea-pig[1]. To date neither fluoroscopic[2–3] nor electromyographic studies[4] have been able to show such opposing motility patterns in the rabbit, and research continues to solve the enigma of the two kinds of faeces production.

As early as 1925, a role in scybala formation for the thick-walled spindle-shaped *fusus coli* located between the proximal haustrated and distal undifferenciated colon was proposed by Auer[5]. More recently, Christensen et al.[6] reported a reversed oral-aboral gradient in the slow-wave frequency of the cat colon. They suggested the existence of a pacemaker area midway along the colon from which slow waves spread towards the caecum tending to polarize flow in the same direction.

This study investigates the possible role of the rabbit's *fusus coli* as an equivalent but more highly differentiated pacemaker area. The electrical activity (slow waves and spike potentials) of the different parts of the colon was recorded from chronically implanted electrodes in normal animals and after surgery to bypass the *fusus coli.*

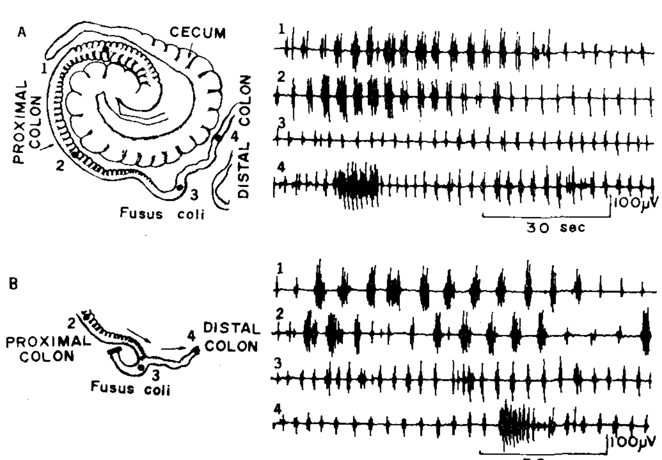
Methods. 6 female rabbits weighing at least 3 kg and on a daily regimen of 1 meal supplied from 08.00 to 12.00 h were used. After a fast of 36 h, the animals were anaesthetized by pentobarbital sodium (20 mg/kg) and chronically implanted with paired electrodes fixed at predeterminated intervals[7] along the different parts of the colon, namely oral (3 taeniae) and aboral (2 taeniae) segments of the proximal colon, *fusus coli* and distal colon. The animals were housed in individual cages and the periods of reingestion of softs faeces were directly observed during the afternoon from 14.00 to 20.00 h each day. Commencing 4 days after surgery, the electrical activity was recorded on a polygraph (Alvar, Paris) at a paper speed of 2.5 mm/sec for individual periods of 24 h for 2 weeks.

Each animal was then reanaesthetized and transection of the colon orad to the *fusus coli* performed. The continuity of the bowel was remade by a terminolateral anastomosis. For each subject, four 24-h recording periods were made again over 2 weeks. Positions of the electrodes were noted at post mortem and recorded as a percentage of total length of the colon.

Results. Feeding always induces the expulsion of hard pellets during the first 4 h, then during the next 4 h soft faeces. This time relationship and alternation of faeces type was characteristic. Production of soft faeces still occurred after surgery to bypass the *fusus coli* but differentiation of the two kinds of faeces was less distinct. No changes in slow wave frequency was observed during the period of feeding and those of the emission of hard or soft faeces.

In all subjects, slow waves at a mean frequency of about 20/min were recorded from the distal colon. On the proximal colon their frequency varied: 13.3/min near the caeco-colic junction, 16.4/min on the oral part, 17.5/min on the aboral part and 19.3/min on the *fusus coli.* Spiking activity occurred either as series of bursts, each of 1–2 sec duration and the same frequency as the slow waves, or as a single prolonged burst lasting 4–7 sec and rapidly propagated over the entire colon. Following this latter activity, the slow-wave frequency of the proximal colon near the junction was at times reduced by half for 1 or 2 min. Reversed contractions propagated from the proximal colon to the caecum also occurred but were only recorded from the oral (3 taeniae) part.

Section of the colon orad to the *fusus coli* was followed by a marked decrease in slow-wave frequency to values of 10–12/min (Figure and Table). Spiking activity was



Schematic diagram of the rabbit's large intestine and corresponding electromyographic record from: A) the proximal colon (1–2), the *fusus coli* (3) and the distal colon (4); B) the *fusus coli* region after section at the termination of haustrated proximal colon and terminolateral anastomosis with the distal colon. Note the reduced slow-wave frequency orad to the anastomosis emphasized by the superimposed spike bursts.

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Slow-wave frequency before and after transection of the colon orad to the *fusus coli* (mean ± SD values for recordings taken during 3 periods of 24 h in 6 animals)

	Proximal colon			*f. coli*	Distal colon		
	3 taeniae		2 taeniae				
Percentage of total colon length	0–10	11–20	21–30	31–40	41–50	51–60	61–70
Slow-wave frequency	14.9	16.4	17.2	21.9	22.1	21.0	20.4
Control	1.3	1.6	0.9	2.1	2.4	2.3	4.6
Slow-wave frequency after section							
1st week	10.7 [a]	11.7 [a]	12.3 [a]	19.6	20.4	18.7	20.4
	2.7	1.4	1.9	2.1	3.6	2.7	2.9
2nd week	12.1 [a]	12.4 [a]	13.2 [a]	19.1	20.4	18.0	18.8
	0.9	0.9	1.1	1.4	1.4	3.2	2.4

[a] $p < 0.01$.

more or less unchanged in intensity. Contractions were propagated to the distal colon from the *fusus coli* either directly or from the proximal colon through the anastomosis.

Discussion. These results show clearly that the *fusus coli* acts as a pacemaker 'pulling up' the slow-wave frequencies of the proximal colon, those of the distal colon maintaining this high level. Thus, the gradient of the slow waves on the proximal colon is the reverse to that seen on the small intestine.

To date there is no valid explanation for the mode of production of the two kinds of faeces. Variable retention of water during the flux and reflux of digesta between caecum and the oral part of the proximal colon has been suggested, but no significant changes in the contractions of the latter region concomitant with production or expulsion of one or other kind of faeces has been detected[4,7].

The polarity of wall movement imparted by the slow waves on the proximal colon demonstrated here would tend to maintain the contents at this level for the optimal period of time. The passage of soft faeces aborad to the *fusus* would simply require a predominance of the spiking activity over the slow-wave counter-current. This work does not explain the dynamics of segregation of soft and hard faeces but suggests that the initial postprandial expulsion of hard faeces situated in the distal colon is the prerequisite for the transit of soft faeces through the *fusus coli*.

High Altitude Influence on the Level and Turn-Over Time of Cardiac Norepinephrine in Rats

M. PRIOUX-GUYONNEAU, J. DURAND, J. R. RAPIN and Y. COHEN

Laboratoire de Pharmacodynamie, Faculté de Pharmacie, Rue Jean-Baptiste Clément, F–92290 Chatenay-Malabry (France), 9 February 1976.

Summary. In rats exposed to an altitude of 2,900 meters the level of endogenous cardiac norepinephrine decreases after the 5th day of exposure. The turner-over time of the amine proceeds in 3 steps which are probably related to periods of stress and adaptation: initial increase, important decrease from the 5th day and return to a normal value from the 12th day.

An insufficient oxygen supply induces hypoxia in man and animals. This state can be provoked by any physiological alterations or by improverished oxygen environment. These conditions are specially realized at high altitude when a decrease of barometric pressure produces reduction of partial pressure of oxygen in the inhaled air (PI 0_2). Most of the studies about physiological consequences of hypobaric hypoxia deal with respiratory and cardiovascular modifications[1–3]. Recently, some authors pointed out that hypoxia, from varioux origins, can be considered as a stress which induces a stimulation of the sympathetic system in adrenals[4–6], heart[7] and brain[8]. Until now, few investigations were made about these effects in hypobaric hypoxia. However it is important to define physiological disturbances under these conditions, for they are likely to be different from those observed in hypoxic hypoxia[9].

To obtain physiological conditions of man living at high altitude, experiments reported in this study were performed at Pic du Midi de Bigorre, France (2,900 m). Influence of hypoxia on noradrenergic system was investigated in the rat by the determination of tissue level and turnover time of cardiac norepinephrine for periods ranging up to 12 days.

Material and method. Male Sprague-Dawley rats (average weight 250 g) were reared at sea level and transferred to an altitude of 2,900 m. During 12 days the animals

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