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PROPAGATION OF ELECTRICAL SPIKING ACTIVITY ALONG THE SMALL INTESTINE: INTRINSIC VERSUS EXTRINSIC NEURAL INFLUENCES

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SUMMARY

1. The electrical activity of the small intestine of conscious dog, recorded by means of chronically implanted electrodes, was related to the transit time estimated by phenol red infusion and its propagation observed after a single or double transection and following either isolation or removal of a 50 cm jejunal loop.

2. In the fasted dog, the activity was characterized by the propagation of myo-electric complexes at a velocity of 4 cm/min during which the mean transit time averaged 13 min/m. About 2/3 of these complexes were seen to pass beyond a single section and anastomosis of the jejunum with a delay of 15 min. This number was reduced to 1/3 and the delay doubled when a second section was performed 50 cm distally.

3. In dog with an isolated jejunal loop, most of the myo-electric complexes were seen to pass from the proximal intestine to the loop and then to the intestine beyond the site of anastomosis within 37 min. Some complexes however passed directly through the anastomosis within 30–32 min, affecting or not the loop. Others started on the loop and/or on the intestine beyond the anastomosis. Finally, the total number of complexes recorded on the distal jejunum was greater than on the duodenum, an effect which disappeared after removal of the isolated loop.

4. The propagation of the complexes occurred at a lower velocity after denervation of a jejunal segment *in situ* but was arrested in the case of an isolated-denervated jejunal loop.

5. It is concluded that continuity of structures in the bowel is essential for the propagation of a myo-electric complex which is stopped and replaced by another complex at the level of an anastomosis, the number of complexes reorganized beyond an anastomosis and their velocity of propagation depending upon both intrinsic and extrinsic neural influences.

INTRODUCTION

It has been recently shown that in several species the migrating myo-electric complex earlier defined as spike potentials recurring as a cyclic sequence of events in the fasted dog (Szurszewski, 1969) is not merely an 'interdigestive housekeeper' (Code & Schlegel, 1974). At any one site the migrating myo-electric complex consisted of a prolonged period of bursts of action potentials superimposed on some

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slow waves (irregular spiking activity) followed by a shorter period when every slow waves have a burst of action potentials superimposed on it (regular spiking activity). A progressive increase in flow occurred during the irregular phase and at the transition to the regular phase the flow became continuous (Bueno, Fioramonti & Ruckebusch, 1975).

Clearly the migrating myo-electric complex is of considerable importance for the understanding of the motor profile of the small intestine. But how is it controlled? Carlson, Bedi & Code (1972) prepared dogs with an isolated 30 cm jejunal Thiry-Vella loop and reported, 'All phases of the complex were propagated distally and most of the complexes after passing distally along the segment orad to the anastomosis were detected in the loop and then in sequence in that portion of the bowel distal to the anastomosis.' Thus they concluded that propagation of the complex involved only the extrinsic nervous system and that the continuity of the bowel was not necessary. Using both dogs and sheep, Grivel & Ruckebusch (1972) also described the orthodromic propagation across isolated or reversed segment of jejunum. They showed however that the regular spike activity might be arrested or jump directly across an intestinal anastomosis thus involving participation of the intrinsic nervous system. Furthermore, long-term recordings of the electrical activity in the dog showed surprisingly that the number of regular spike phases recorded on the distal jejunum after isolation of a jejunal Thiry-Vella loop was higher than that recorded orad to the anastomosis (Bueno & Praddaude, 1978).

The present study was undertaken to investigate the role of the continuity of the bowel *versus* extrinsic neutral influences in the propagation of mygrating myo-electric complexes and their control of propulsion of the digesta.

METHODS

The propagation of the migrating myo-electric complex was measured in twenty-six dogs weighing from 19 to 28 kg from pairs of electrodes (insulated nichrome wires, 120 μm in diameter, 2 mm apart, 50–100 cm long) implanted under thiopentone anaesthesia at different sites in the jejunum. Each wire was inserted through the serous and muscular layers using a curved needle as a trocar tying off the free end close to the intestinal wall (Bueno *et al.* 1975). Animals were placed in modified metabolism cages which allowed free movement but assured sufficient restraint for long-term recordings which began one week after surgery and continued for periods of 10–30 days. The electrodes were connected to an e.e.g. machine (Reega VIII, Alvar, Paris) and a paper speed of 2·5 mm/sec was used. Slow waves were eliminated by a high-pass filter and the level of remaining activity was automatically plotted by means of a six-channel integrator connected to a potentiometric recorder. The percentage of spike activity during the recording time was determined by direct inspection of the integrated record and the phase of regular spiking activity identified as those of high amplitude.

First series (ten dogs)

Eight pairs of electrodes were positioned beyond the ligament of Treitz at intervals of about 10 cm in each dog. In dogs 1–3 a catheter was inserted into the lumen of the intestine at the second electrode site (15 cm beyond the ligament of Treitz) and a T-shaped cannula fitted in the intestine at the eighth electrode site (60 cm aboral to the catheter).

Transit times were measured every 2 days in dogs 1–3 throughout a 10-day recording period. A phenol red bolus (1 ml. containing phenolsulphonphthalein – PSP) was rapidly injected through the catheter when the activity corresponding to the regular phase of migrating myo-electric complex was recorded on the first group of electrodes, i.e. 1–2 min before its arrival at the injection

site, 10 cm aborally. This injection was made during a continuous polyethylene glycol (PEG) infusion (1 % solution, mol. wt. 4000).

The total flow of intestinal contents at the site of cannula (f_t) was determined from both the concentration of PEG (c) in samples taken at this level every 2 min and that of PEG infusion (C) at a rate (F) of 3 ml./min. The following relation f_t (ml./min) = $(F \times C)/c$ was used and the flow rate of digestive contents (f) determined as $f = F(C-c)/c$.

The mean transit time of the phenol red bolus (MTT) was calculated from the PSP concentration profile as the time from injection of PSP to peak PSP concentration (Bueno *et al.* 1975).

All the ten dogs were then reanaesthetized. The jejunum was transected and anastomosed at 40 cm from the ligament of Treitz, that is between the 3rd and 4th electrode sites. Six additional pairs of electrodes were positioned in dogs 4–6 at 1, 2 and 3 cm before and beyond the anstomosis. Recordings were made in all animals and transit times measured again for 10 consecutive days starting 1 week after surgery.

In dogs 7–10, a third operation was performed. The jejunum was transected and anastomosed 50 cm below the first anastomosis, that is 5 cm beyond the eighth electrode site. Another 10-day recording session was then performed in these dogs. The intervals between electrode sites were examined and measured post-mortem in all animals.

Second series (ten dogs)

Six pairs of electrodes were inserted in each dog, respectively at 15, 35, 45, 85, 95 and 115 cm from the ligament of Treitz. After a 10-day recording session 1 week after surgery, the jejunum was transected at 40 and 90 cm from the ligament of Treitz and anastomosed (dogs 11–13), isolated as a Thiry-Vella loop (dogs 14–17) or the segment removed (dogs 18–20). The recordings were continued for 1 week after surgery for 30 days in all animals. For the dog 17, the Thiry-Vella loop was removed during a third operation and recordings continued again for 10 days, 1 week later.

Third series (six dogs)

Three animals (dogs 21–23) were implanted with six pairs of electrodes, two of them fixed on an isolated jejunal loop. The jejunal segment was placed under the skin and after 1 month, both nerves and vessels were cut. Recordings were continued for a period of 30 days 1 week after isolation. In dogs 24–26, the continuity of the bowel was maintained, but a 100 cm segment of the jejunum (from 50–150 cm beyond the ligament of Treitz) was denervated by sectioning all the nerves along the mesenteric arteries. Each branch of the mesenteric artery close to the jejunal wall was gently pulled using a thread immediately removed after denervation. In addition, the extrinsic nerves which accompanied the mesenteric arteries before their division for this area were again sectioned. Six pairs of electrodes were fixed, two pairs were placed at intervals of about 20 cm orad to the denervated segment, on the segment and aborad to it. The intervals between electrode sites were measured post-mortem. No signs of ischaemic damage were detected from a visual inspection of both the muscular coat and the mucosa.

Analysis of results

Continuous 24 hr records were made during each 10-day recording period. All complexes during this period were taken into account. Results are usually expressed as mean ± S.D.

RESULTS

First series of experiments

Propagation of the myo-electric complex following transection and re-anastomosis. All dogs of the first series had cyclically recurring myo-electric complexes (migrating myo-electric complexes) from 16 to 24 hr after feeding. Each complex which lasted about 60 min, showed two successive phases: irregular bursts of spike potentials often propagating rapidly between two sets of electrodes and a phase of regular bursts of

spike potentials occurring during 3–9 min at the frequency of the slow waves. The recurring interval between the phases of regular spiking activity was 83·0 ± 24·2 min (mean ± S.D.) and the number of complexes averaged 69·1 ± 9·1 (mean ± S.D.) per dog during a 10-day recording period (Table 1).

TABLE 1. Alterations in the number of migrating myo-electric complex propagated along the small intestine (mean values ± S.D. for a 10-day recording period)

Dog no.	Control	Orad	Aborad	%
		Section at 40 cm from the LT*		
1–10	69·1 ± 9·1	68·9 ± 8·7	49·7 ± 4·9	(72·1)†
		Section at 40 and 90 cm from the LT		
	Orad	Aborad 1st section	Aborad 2nd section	
11–13	68·6 ± 14	39·1 ± 7·6	21·9 ± 6·9	(31·9)
		Isolation of a 50 cm Thiry-Vella loop		
	Orad	On the loop	Aborad	
14–17	73·0 ± 7·4	61·3 ± 2·0	83·6 ± 7·7	(114·5)
		Resection of a 50 cm jejunal segment		
	Orad		Aborad	
18–20	65·5 ± 11·3		31·5 ± 5·5	(48·1)
		Isolation of a 50 cm loop under the skin		
	Orad	Loop	Aborad	
21–23	60·2 ± 4·2‡	30·2 ± 4·1	36·1 ± 3·2	(60·0)
		Denervation of a 100 cm jejunal segment		
	Orad	Segment	Aborad	
24–26	68·2 ± 8·7	48·1 ± 6·1	40·7 ± 4·7	(59·7)

* Ligament of Treitz.

† Indicates the percentage of duodeno-jejunal migrating myo-electric complex still recorded on the distal part of the jejunum after section, isolation, resection or denervation.

‡ Significantly different at $P < 0·05$ from control values.

After transection and anastomosis at 40 cm, the orderly development of the migrating myo-electric complex persisted but some phases of regular spiking activity recorded on the proximal jejunum faded out at the anastomosis. The number of these phases observed beyond the anastomosis during a 10-day recording period was 28 % less than that recorded orad to the section. Furthermore, a delay of 8–20 min occurred as the phase of regular spiking activity seemed to pass from the electrode site before to the electrode site beyond the anastomosis in dogs 1–3 (Fig. 1). When a second transection was performed 50 cm aborally (dogs 7–10), the number of phases of regular spiking which faded out at the 1st anastomosis was increased and the delay taken by a migrating myo-electric complex to pass the 1st anastomosis was then nearly doubled.

In dogs 4–6 which had three additional pairs of electrodes 1, 2 and 3 cm before and after the anastomosis, the phase of regular spiking activity of the migrating myo-electric complex which passed through the anastomosis was strongly reduced in

duration 2 and 1 cm orad to the anastomosis. Beyond the anastomoses this phase was absent at 1 and 2 cm and lasted only 3–4 min at 3 cm. The duration of both phases (irregular and regular) recorded at 5 cm aborad to the anastomosis was still slightly reduced and the normal pattern occurred on the more distal electrode site. As shown by Fig. 2, the delay seen in the passage of the phase of regular spiking activity across

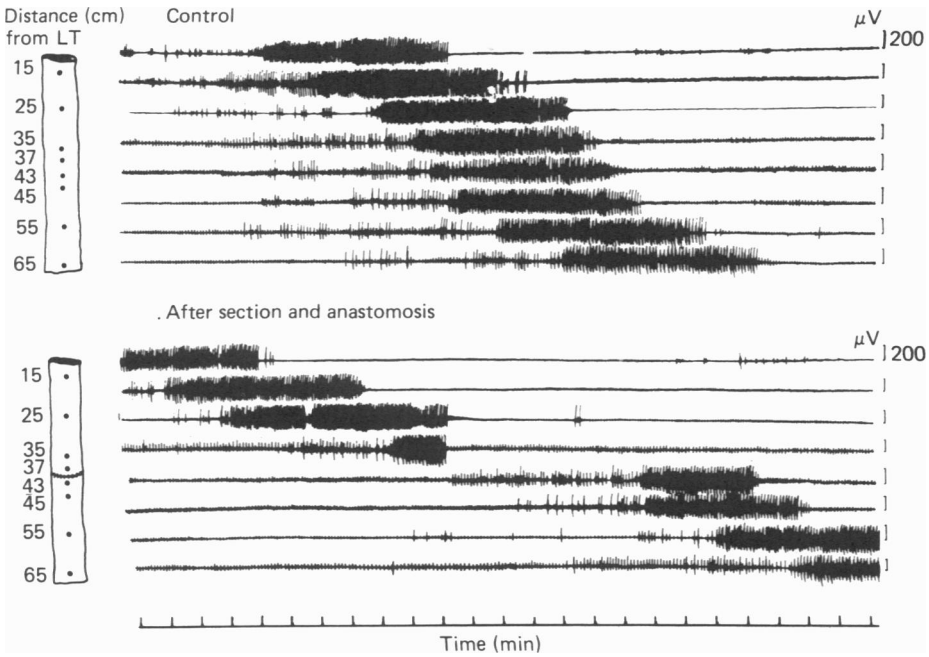

Fig. 1. Propagation of the phase of regular spiking activity along the jejunum from 15 to 65 cm beyond the ligament of Treitz (LT). After a jejunal transection, the mean velocity of propagation was unchanged except that a delay of about 10 min occurred at the anastomosis in this experiment.

the anastomosis was not related to a reduction in the velocity of propagation but to an interruption of the propagation, another phase of regular spiking starting 3–5 cm beyond the section.

Transit time following transection. In dogs 1–2, the migrating myo-electric complex pattern was not altered by the infusion of PEG before or after transection. Some disorganization of the pattern was observed in dog 3 and the results disregarded. For a PSP bolus given 30–60 sec before the phase of regular spiking the transit time averaged 12·5 min/m and varied between 7 and 18 min/m in ten trials and the digesta flow of contents averaged 56 ± 13 ml./min. After transection and anastomosis, the mean digesta flow was unchanged but the mean transit time increased to 21 min/m with values ranging between 16 and 27 min/m. The delays in the occurrence of the PSP concentration peak at the cannula level after transection are shown in Fig. 3 for the trials performed in dogs 1 and 2.

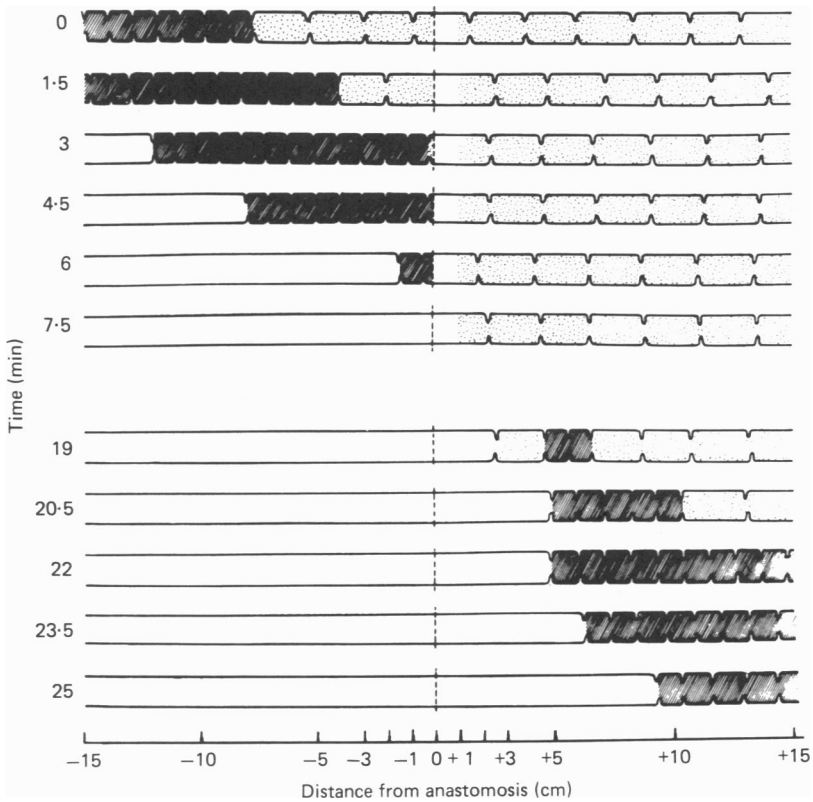

Fig. 2. The disappearance of the regular spiking activity (RSA) at a jejunal transection and anastomosis and its reorganization beyond. The diagram shows the jejunum from − 15 cm above to + 15 cm below the anastomosis at different times (0–25 min) after the appearance of a period of regular spiking activity (hatched area) at the end of a period of irregular spiking (dotted area). The length of intestine showing regular spiking activity at one time decreases progressively up to the anastomosis. No such activity occurs 0–4 cm beyond the anastomosis (time 7·5 min) but it does reappear, at + 4 cm at 19 min, 12 min after its disappearance above the anastomosis and progressively occupies a greater length of jejunum.

Second series of experiments

Propagation following jejunal resection. These ten dogs showed cyclically recurring myo-electric complexes on the proximal jejunum and their number was not significantly changed at this level after double transection, isolation or removal of a 50 cm jejunal segment. About 70% of the phases of regular spiking did not reach the distal jejunum after a double section (dogs 11–13) and the total delay in their passage through the two anastomoses was nearly three times that seen for a single anastomosis (Table 2). After isolation of a Thiry-Vella loop, the number of phases of regular spiking activity recorded beyond the anastomosis was significantly increased (83·6 ± 7·7 *vs.* 73·0 ± 7·4 for 10-day recording session in dogs 14–17). After removal of the Thiry-Vella loop in dog 17, the number of the such phases propagated across the anastomosis was only 50% of that recorded on the proximal jejunum as for dogs 18–20 (see Table 1) in which a 50 cm jejunal segment was resected.

Mechanism of increased activity following isolation. A detailed analysis of the records obtained in dogs 14–17 showed that some phases of regular spiking faded out at the anastomosis. About 60% of the propagated phases occurred in the loop in sequence with the rest of the bowel (Fig. 4). Nearly 30% of the propagated phases migrated directly across the anastomosis without affecting the loop as shown in Fig. 4. The remaining phases propagated directly through the anastomosis within 30 min and also affected the loop with a delay of 34 min so that two phases might be recorded simultaneously, one on the loop and another beyond the anastomosis (see Fig. 4). Some of the phases seen on the loop might 'jump' from the distal end of the loop to the intestine. In

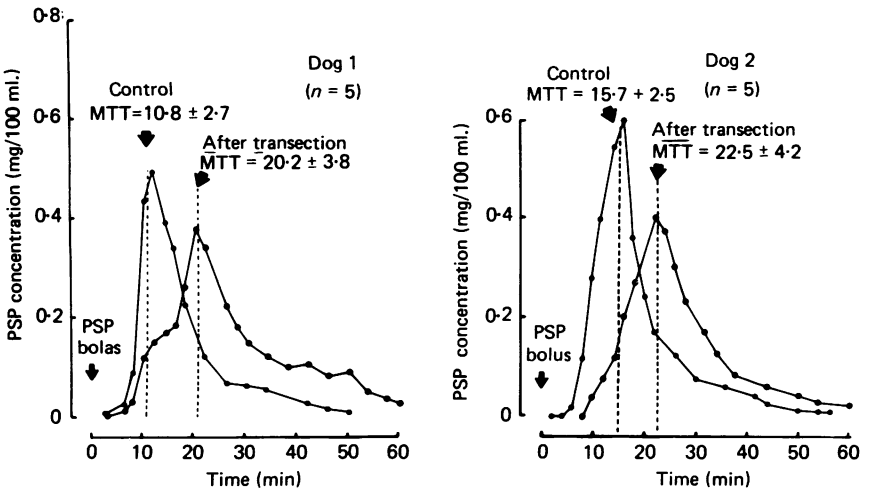

Fig. 3. Velocity of PSP bolus and mean transit time (MTT) before and after jejunal transection and anastomosis. The MTT calculated as the time from PSP bolus injection to peak of the PSP concentration profile at the jejunal cannula and velocity of bolus from the jejunal catheter to the jejunal cannula (60 cm) are nearly halved in dog 1 and by 30% in dog 2 after transection and anastomosis 40 cm from the ligament of Treitz.

TABLE 2. Delays at which the phases of regular spiking activity were recorded distally after section, excision and denervation (mean values ± S.D. for 10-day recording periods)

Dog no.	Section from the LT (cm)	Delay (min)
1–10	40	15·2 ± 2·6
11–13	40	32·1 ± 1·3 at 40 cm
	90	17·1 ± 2·7 at 90 cm
14–17	Thiry-Vella loop	To the loop and from the loop 17·1 ± 3·1 and 20·2 ± 3·7 (Fig. 4*A*) Across the anastomosis 32·7 ± 2·9 (Fig. 4*B*) Across the anastomosis and to the loop 30·1 ± 3·6 and 34·6 ± 4·1
18–20	Excision of a 50 cm loop	25·2 ± 2·8
21–23	Isolated loop under the skin	To the loop and from the loop 15·1 ± 3·1 and 15·0 ± 6·1 Across the anastomosis 25·4 ± 3·1
	Isolated-denervated loop	Across the anastomosis 30·3 ± 6·1

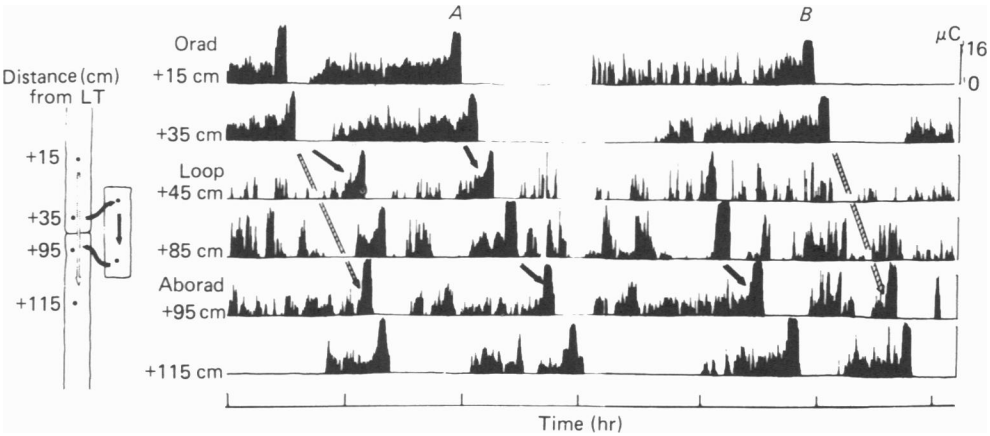

Fig. 4. Electrical spiking activity of the jejunum integrated at 20 sec intervals after isolation of a jejunal Thiry-Vella loop (50–90 cm from the ligament of Treitz). Positions of electrodes are shown diagrammatically to the left of the records. The migratory myo-electric complex may pass directly through the anastomosis (hatched arrow) and to the loop (filled arrow). Usually the complex would pass to the loop and back to the normal intestine (filled arrows) or directly through the anastomosis without affecting the loop. A complex may also start in the proximal part of the loop and pass to the normal intestine.

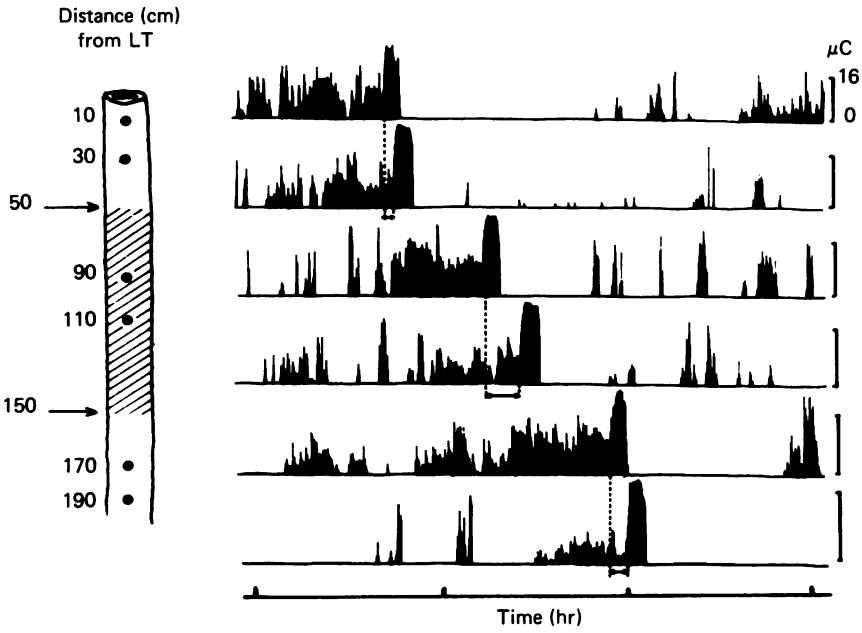

Fig. 5. Propagation of the migrating myo-electric complex slows through a denervated segment of jejunum. Electrical activity integrated at 20 sec intervals. Position of electrodes are shown to the left of the records. Denervation of a 1 m segment of jejunum by section of the mesentery and mesenteric nerves along the corresponding arteries decreases the velocity of propagation through the denervated segment.

addition, from one to three phases per day started on the proximal end of the loop, independently of the rest of the bowel and then migrated back to the intestine (see Fig. 4). Obviously, these two possibilities may account for the increase in number of the such phases recorded beyond the anastomosis.

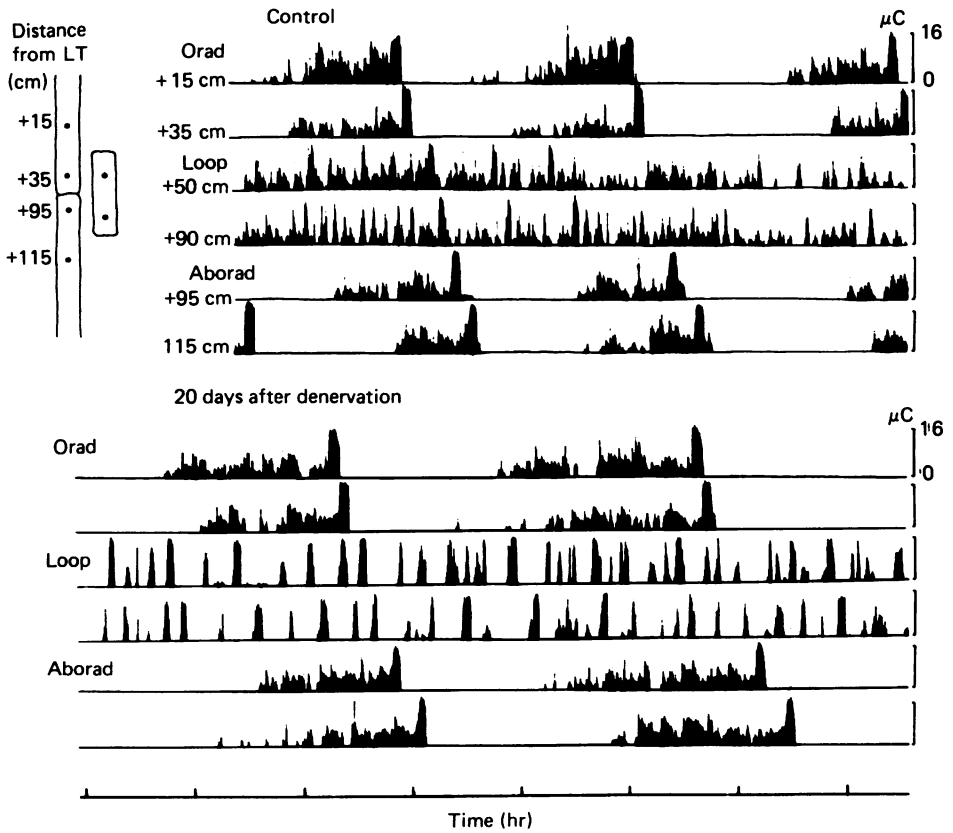

Fig. 6. After extrinsic denervation, a jejunal loop shown an autonomous rhythm of regular spiking activity. Electrical spiking activity integrated at 20 sec intervals is recorded from electrodes on the duodenum and on the isolated loop (40–90 cm from ligament of Treitz). Positions of the electrodes are shown on the diagram to the left of the records. Before denervation, the complex was propagated through the loop back to the anastomosed jejunum or directly through the anastomosis. After section of vascular and nervous pedicles to isolate the loop, numerous phases of regular spiking activity occur, only transmission of the complex through the anastomosis occurred.

Third series of experiments

Denervation of a jejunal segment. Section of the mesentery and of the nerves which accompanied five to six branches of the mesenteric artery reduced the number of propagated complexes and their velocity of propagation. The number was reduced by 40% and the velocity of propagation of the remaining regular spiking activity phases was reduced from 4 to about 1 cm/min (Fig. 5). The velocity was again increased to 2–3 cm/min distally to the denervated area.

Denervation and isolation. When a 50 cm jejunal segment was isolated and placed under the skin, nearly continuous irregular spiking activity was recorded and the number of complexes recorded on the proximal jejunum was slightly reduced, and about 50% of the complexes faded out at the level of anastomosis. The remaining regular spiking activity phases were seen to pass either on to the loop or directly across the anastomosis without affecting the loop. The absence of quiescence following the passage of a phase of regular spiking made some recordings unreliable (Fig. 6). After denervation and revascularization, the majority of the regular spiking phases passed directly across the anastomosis. By contrast, the isolated-denervated loop behaved as an independent unit showing at intervals of $22{\cdot}5 \pm 6{\cdot}7$ min short phases of regular spiking activity lasting $4{\cdot}7 \pm 0{\cdot}6$ min.

DISCUSSION

The occurrence and propagation of the migrating myo-electric complex is clearly seen by recording the 20 sec integral of spiking activity at low speed. By continuous recording for a relatively long period, during which a relatively large number of complexes will have occurred, it is possible to obtain an accurate view of changes in the number and propagation of complexes after transection and anastomosis isolation of a loop, excision of a duodenal segment, or denervation. In addition, surgery of the jejunum as detailed above does not impair the frequency of propagation of the myo-electric complex on the intestine proximal to the jejunum. A normal frequency of the migrating myo-electric complex was also observed on the proximal jejunum of dogs with a 30 cm isolated segment (Carlson *et al.* 1972) or even after a 75% jejuno-ileal bypass (Schang, Dauchel, Marescaux, Mougin, Angel & Grenier, 1978).

Our results show as expected that complexes can pass to an isolated 50 cm Thiry-Vella loop. However, that interpretation seems more complex than it has previously been suggested. Carlson *et al.* (1972) analysed twenty-two complexes from four dogs in detail; fifteen passed in sequence from the electrodes orad to the anastomosis to the loop and then to the electrodes distal to the anastomosis; we found the proportion propagated to the loop in the same range, forty-eight out of seventy-three complexes in dogs 14–17 (Fig. 4). In the remaining complexes of their series, Carlson *et al.* observed that the migrating myo-electric complexes were early by 15–23 min or late by 10 min. We show that complexes can be initiated *de novo* on the isolated Thiry-Vella loop (Fig. 4) and these new complexes initiated on the loop can pass back to anastomosed bowel – one reason why the number of myo-electric complexes on the ileum is greater than on the duodenum in a dog with a Thiry-Vella loop (Table 1).

Some complexes do seem at first sight to pass directly across the anastomosed bowel although with some delay (Table 2) both with transection and anastomosis and with transection, isolation or removal of a 50 cm segment and anastomosis. A striking feature is that the phase of regular spiking activity is not seen just beyond the anastomosis and the duration of this phase before the anastomosis is decreased. We suggest then that the myo-electric complex does not propagate across the anastomosis but that a new phase of regular spiking is organized beyond the transection and anastomosis. Two factors may bring about the re-organization: an excitatory reflex through extrinsic nerves similar to that causing the complex in the Thiry-Vella

loop; the regular spiking activity before the anastomosis causes a local excitation of tonic and phasic receptors by changes in pressure beyond the section. Such an hypothesis is in agreement with the local reflexes elicited by the bulk of digestive contents in sheep fitted with two cannulas at an interval of 4 m on the jejunum, the decrease or increase in spiking activity duration owing to bypass or increased flow respectively (Ruckebusch & Bueno, 1977).

A double transection caused a greater decrease in the number of complexes beyond both anastomoses and a delay at both anastomoses. That the delay to pass the first anastomosis increased after a second anastomosis was performed as well as a decrease of propagated regular spikes could be due to the removal of the 'permissive' effect from the distal part of the gut on its orad activity via intrinsic nerves or the properties of the smooth muscle itself.

However, transection and anastomosis of the bowel will not disrupt the extrinsic neural influences which caused propagation of the migrating myo-electric complex to an isolated Thiry-Vella loop. Can the complex reorganize beyond the transection and anastomosis in the absence of the extrinsic reflex? The extrinsic reflex should not be effective beyond the anastomosis in those preparations where 50 cm of bowel was removed or made into an isolated loop. The complex is reorganized by stimulation of phasic and tonic receptors in the bowel wall alone. Such complexes also occurred in a 50 cm denervated segment of jejunum. It was possible however to prevent its reorganization. If a loop of intestine was isolated under the skin, complexes similar to those in a Thiry-Vella loop occurred. But if after allowing revascularization the mesenteric blood vessels were cut, there was no pattern on this denervated loop. Neither could there occur a reorganization of the complex through the extrinsic nervous system or distension. A situation in which no circulatory changes could be involved is that of a denervated double transected length of intestine that is still in continuity with the rest of the gut. Such a segment also behaved as an independent unit showing nearly continuous spiking activity at a low intensity with numerous phases resembling those of regular spiking activity (unpublished observations). In addition, the pattern was complicated by the superimposed spiking activity due to the passage of digestive contents across the anastomosis at the occurrence of a migrating myo-electric complex.

Another point to be mentioned is that for the regular spiking phase; spike bursts are superimposed on each slow wave, and thus that its velocity of propagation is related to the slow-wave frequency which decreased from 20 to 15/min along the dog's intestine in a stepwise fashion (Diamant & Bortoff, 1969). When the duodenum or proximal jejunum are transected, the frequency distal to the line of section falls precipitously to a level similar to that of the ileum (Milton & Smith, 1956; Code & Szurszewski, 1970), a slow progressive recovery occurring within 2 months after section (Grivel & Ruckebusch, 1971). Such an adaptation was observed too for the motility in both rats (Weser & Hernandez, 1971) and dogs (Schang *et al.* 1978). Although these experiments were not made for this purpose, it is likely that the reorganization of the phases of regular spiking activity beyond an anastomosis represents an adaptative factor for the propulsion of digesta.

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REFERENCES

BUENO, L., FIORAMONTI, J. & RUCKEBUSCH, Y. (1975). The rate of flow of digesta and electrical activity of the small intestine in dogs and sheep. *J. Physiol.* **249**, 69–85.

BUENO, L. & PRADDAUDE, F. (1978). Propagation des complexes myoélectriques et résection intestinale chez le chien. *C. r. Séanc. Soc. Biol.* **172**, 191–196.

CARLSON, G. M., BEDI, B. S. & CODE, C. F. (1972). Mechanism of propagation of intestinal interdigestive myoelectric complex. *Am. J. Physiol.* **222**, 1027–1030.

CODE, C. F. & SZURSZEWSKI, J. H. (1970). The effect of duodenal and midsmall bowel transection interdigestive myoelectric complex of the dog. In *Proc. Fourth Int. Symp. on Gastro-Intestinal Motility*, pp. 631–634. Vancouver, B.C.: Mitchell Press Ltd.

CODE, C. F. & SZURSZEWSKI, J. H. (1970). The effect of duodenal and midsmall bowel transection on the frequency gradient of the pace-setter potential in the canine small intestine. *J. Physiol.* **207**, 281–289.

DIAMANT, N. E. & BORTOFF, Y. (1969). Effects of transection on the intestinal slow wave frequency gradient. *Am. J. Physiol.* **216**, 734–743.

GRIVEL, M. L. & RUCKEBUSCH, Y. (1971). A study on the dog and cat of the electrical activity of the small intestine some months after transection and transplantation of the gut. *Life Sci. Oxford* **10**, 241–250.

GRIVEL, G. W. & RUCKEBUSCH, Y. (1972). The propagation of segmental contractions along the small intestine. *J. Physiol.* **227**, 611–625.

MILTON, G. W. & SMITH, A. W. M. (1956). The pacemaking area of the duodenum. *J. Physiol.* **132**, 100–114.

RUCKEBUSCH, Y. & BUENO, L. (1977). Migrating myoelectrical complexes of the small intestine. An intrinsic activity mediated by the vagus. *Gastroenterology* **73**, 1309–1314.

SCHANG, J. C., DAUCHEL, J., MARESCAUX, J., MOUGIN, C., ANGEL, F. & GRENIER, J. F. (1978). Importance de l'iléon dans l'adaptation motrice de l'intestin après court-circuit jéjuno-iléal. Etude électromyographique. *Gastroentérol. clin. biol.* **2**, 373–382.

SZURSZEWSKI, J. H. (1969). A migrating electric complex of the canine small intestine. *Am. J. Physiol.* **217**, 1757–1763.

WESER, E. & HERNANDEZ, M. H. (1971). Studies of small bowel adaptation after intestinal resection in the rat. *Gastroenterology* **60**, 69–75.