

MYOMETRIAL ACTIVITY AND EXPULSION OF FETUSES

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ABSTRACT

Chronic implantation of extracellular electrodes on successive uterine segments of pregnant miniature sows and marking of their fetuses were performed in order to relate characteristics of uterine electrical activity during delivery with the sequence of expulsion of piglets.

The electromyographs during parturition were characterized by synchronic and well propagated phases of activity that could first appear at any of the four electrodes; however, initiation occurred most frequently at the electrodes on the two extreme ends of a horn. Analysis of the relative occurrence of tubocervically and cervicotubally propagated activity phases indicated that the latter were present, and even could dominate, before and during expulsion of the piglets. The mean duration of the activity phases decreased and their mean propagation-time along the horn increased after emptying of the horn. However, before as well as after completion of delivery, a wide range in propagation-time of even two successive activity phases was measured.

It is concluded that a decrease in uterine volume is responsible for the rather abrupt changes of the characteristics of myometrial activity upon delivery of the piglets from a horn. Possible explanations for the wide range of the propagation-times are discussed and it is suggested that the cervicotubally directed contractions prevents untimely interruption of the fetal-placental-maternal connections of the piglets that are not yet due to be expelled.

INTRODUCTION

While in the past decades much attention has been paid to endocrinological aspects of the initiation of parturition in domestic animals (reviews by Thorburn et al., 1977; Fuchs, 1978), the interest in myometrial function seems to be lost once the cervix has opened and the uterus shows either spontaneous or induced regular contractions. Mechanisms of expulsion of the conceptuses have been studied only in a few (polytocous) species such as the pig (Dziuk and

Harmon, 1969), mouse (Fuller et al., 1976) and dog (Günther, 1955) by marking the fetuses during pregnancy but in none of these studies was myometrial activity recorded simultaneously. Yet at least two apparently contradictory functions have to be performed at the same time by the contracting uterus during labour:

1) expulsion of fetuses from the two uterine horns, 2) the retention of those fetuses that are not yet in turn to be expelled.

The propagation of uterine contractions in either a tubocervical or cervico-tubal direction has been quantified extensively in the oestrous ewe (Hawk, 1975a; Prud'homme, 1976), their relative occurrence being closely related with the rate of sperm transport and fertility (Hawk, 1975b). The presence of these both types of propagation of uterine contractions during parturition has been reported in the rabbit (Csapo and Takeda, 1965; Naaktgeboren et al., 1975), the rat (de Paiva and Csapo, 1973; Schoof and Naaktgeboren, 1978) and the pig (Zerobin and Spörri, 1972) but their relative occurrence has not been quantified and related to the mechanism of expulsion of the fetuses. Because surgical inversion of one or both uterine horns before mating in sows did not affect the subsequent fertility but seriously disturbed the course of labour (Bosc et al., 1976) the pig seems to be an interesting species for studying propagation of uterine contractions.

In the present report, *in vivo* electromyography with surface electrodes implanted on successive segments of one uterine horn was combined with trans-uterine marking of fetuses in pregnant minipigs. The frequency, duration and direction of propagation of phases with electrical discharges during parturition were quantified and related to the emptying of the horn with electrodes.

MATERIAL AND METHODS

Seven miniature sows were laparotomized between D73 and 102 of pregnancy (Day 0 being the day of mating). Fetuses of one or both uterine horns were marked individually with a radiopaque substance by transuterine, intramuscular injections. Surgical details have already been published (Taverne et al., 1977). During the same operation 4 pairs of silver electrodes were sutured at different sites on the outside of the uterine wall; the exact locations will be indicated in the results section. The wires from the electrode were led subcutaneously to the mid-dorsal position where they were exteriorized and connected to a 8-pin plug. Myometrial electrical activity was recorded according to the method described by Naaktgeboren et al. (1973).

Parturition in 5 sows (nrs. III, VII, IX, XIII and XIV) took place between D111 and 114 of pregnancy. One sow (nr. 403) aborted on D98, i.e. 25 days after surgery. The remaining sow (nr. 432) showed nest building behaviour on D113 of pregnancy, i.e. 30 days after surgery. Labour remained nonproductive in this

animal for about 48 hours. On D115 the sow was slaughtered and a 180° uterine torsion was found at autopsy. All piglets had died, their placenta's being detached.

Recording of myometrial activity took place continuously in all sows during labour. At birth each piglet was earnotched with the number of his sequence in the litter. At the first day post partum roentgenograms of each piglet were made for recognizing the marked sites. In this way the origin of each piglet could be established.

The electromyographs during parturition show periods of synchronic potential fluctuations at all four electrodes: these periods will be called "activity phases". Their frequency (per 40 minutes) and durations (sec) were measured. Because all recordings took place with a high constant paper speed (2.5 mm/sec), the propagation of the activity phases along the uterine horn could be analyzed, i.e. the successive appearance of the electrical activity at successively implanted electrodes was noticed. When propagation between at least 3 successive electrodes could be discerned, its direction was established as either tubocervically or cervicotubally. From those activity phases that were propagated between 4 electrodes the time-interval between the start of the activity at the two most distant ones (i.e. conduction-time) was measured (sec).

RESULTS

In 4 sows (nrs. VII, IX, XIII and 432) all electrodes were still functioning during labour.

As demonstrated by Fig. 1, phases of activity could first appear at any of the 4 electrodes along a uterine horn. This was also observed in cases where not all electrodes were originally implanted in the middle of a fetal locus (Fig. 2). The majority of the phases that were propagated between 3 or 4 electrodes first appeared at the two ends of the uterine horn (Table 1). When propagation could be followed only between 3 or 2 electrodes, the others remained inactive or started to be active at exactly the same time (Fig. 1). Occasionally propagation between only 2 electrodes was observed simultaneously at the two halves of a uterine horn. A conspicuous finding was the occurrence of "echo-propagation", i.e. a tubocervically or cervicotubally propagated activity phase continued in the opposite direction (Figs. 1 and 3). This type of propagation was found just before and during expulsion of the piglets from the registered horn.

Figure 4 shows the frequency of the activity phases at the two most distant electrodes in three sows during parturition. The height of the vertical bars indicate the total number of phases that were propagated between 3 or 4 electrodes; the relative distribution of the tubocervically and cervicotubally directed ones

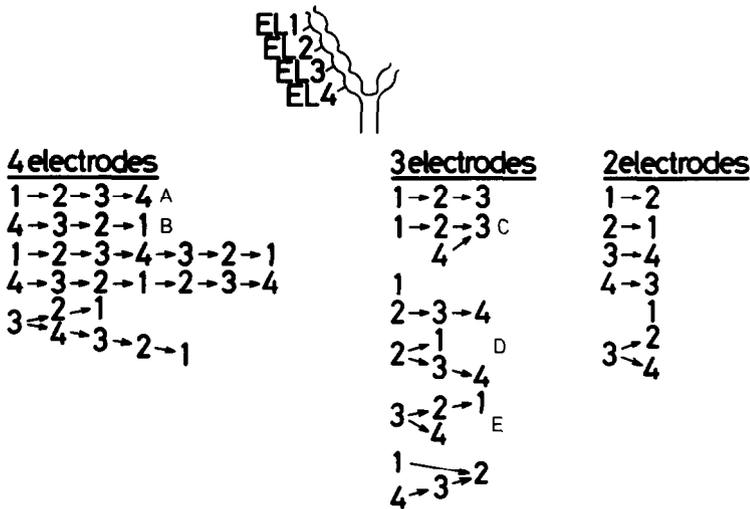


Fig. 1. Different types of propagation of myometrial activity during parturition as judged by the appearance of electrical discharges at successively implanted electrodes (see text). The ones indicated by A, B, C, D and E are illustrated by figure 2.

TABLE 1.

The relative distribution (%) of different types of propagation of myometrial electrical activity phases during spontaneous parturition at normal term in 3 sows. The implantation sites of the electrodes (1, 2, 3 and 4) are given by the diagrams of figure 4.

sow nr	tubocervical direction				cervicotubal direction			
	I→3	I→4	2→4	n (=100%)	4→2	4→I	3→I	n (=100%)
VII	12	78	10	77	13	60	27	15
IX	17	65	18	110	24	73	3	37
XIII	13	80	7	74	18	55	27	33

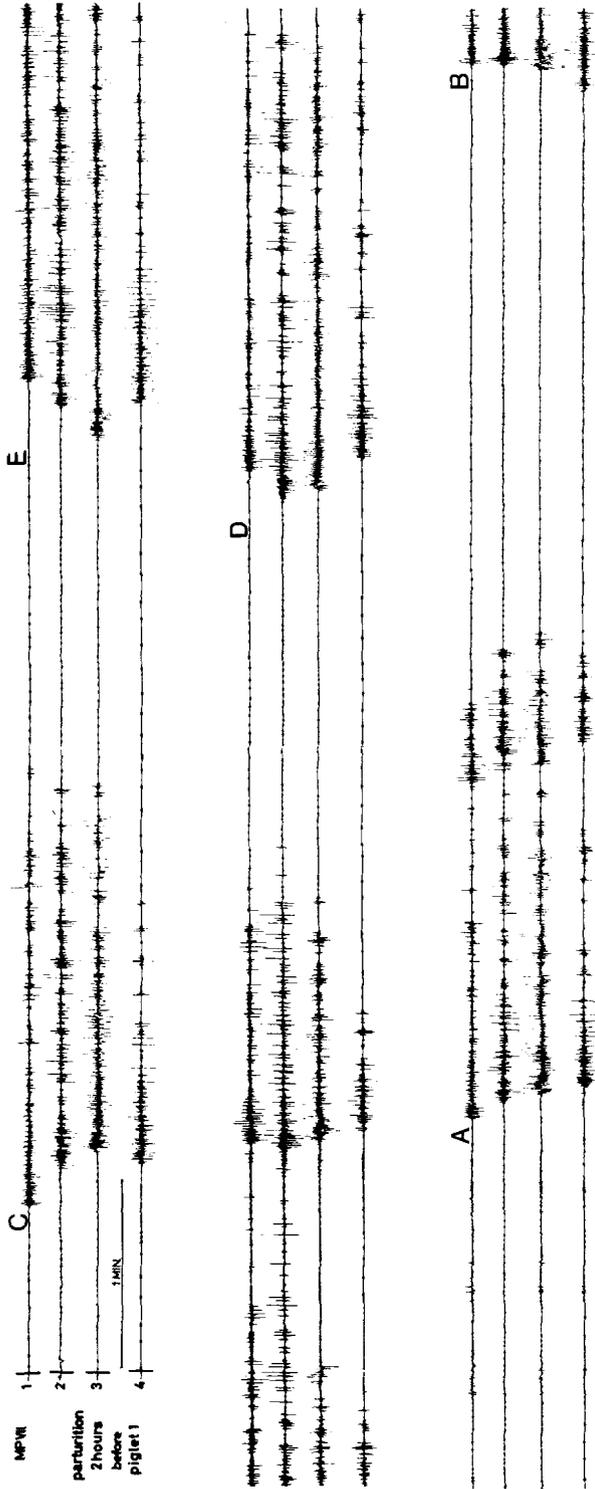
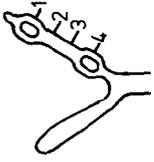


Fig. 2. Uterine electromyograph in three continuous sections from sow VII at 2 hours before delivery of the first piglet. Successive phases of activity first appear at different uterine segments and several types of propagation are recognizable. The diagram shows the relative position of the electrodes.

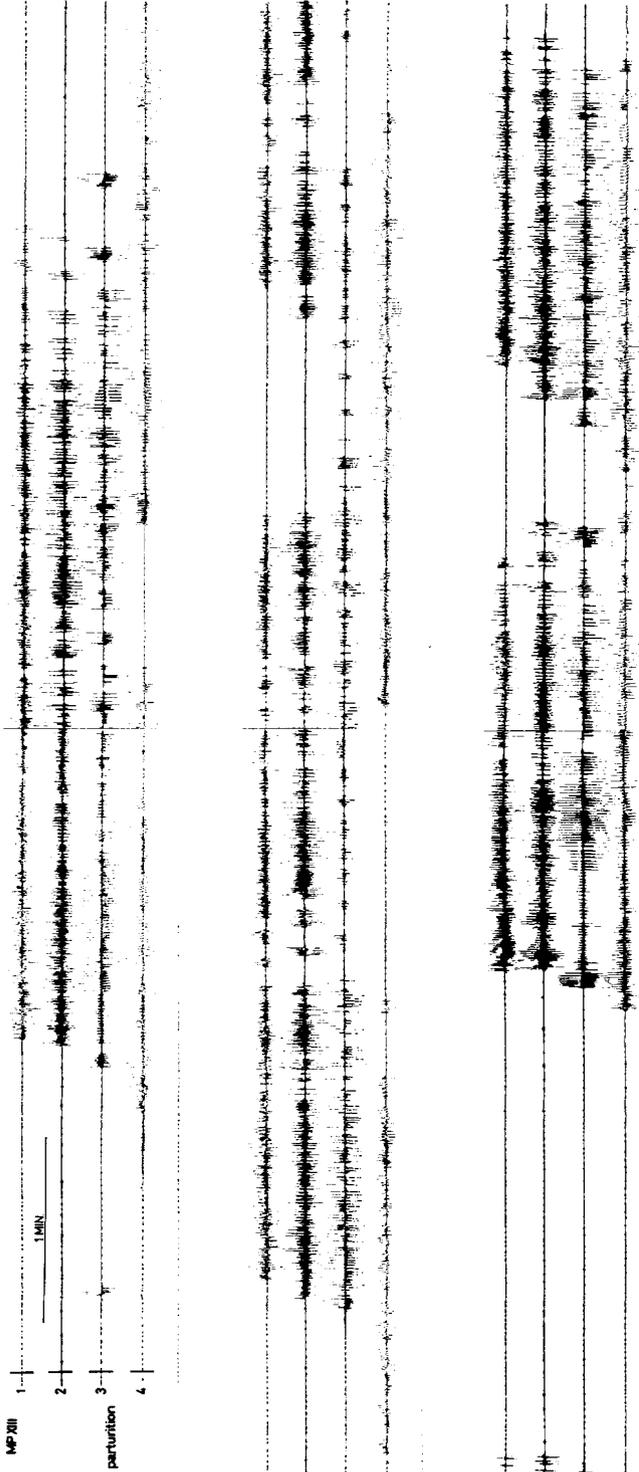
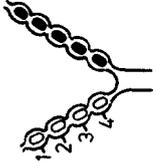


Fig. 3. Uterine electromyograph in three continuous sections from sow XIII at 40 minutes before delivery of the first piglet. So-called "echo-propagated" phases of electrical activity (upper two sections) and two cervicotubally directed ones (lower section) are shown. The diagram indicates the relative position of the electrodes.

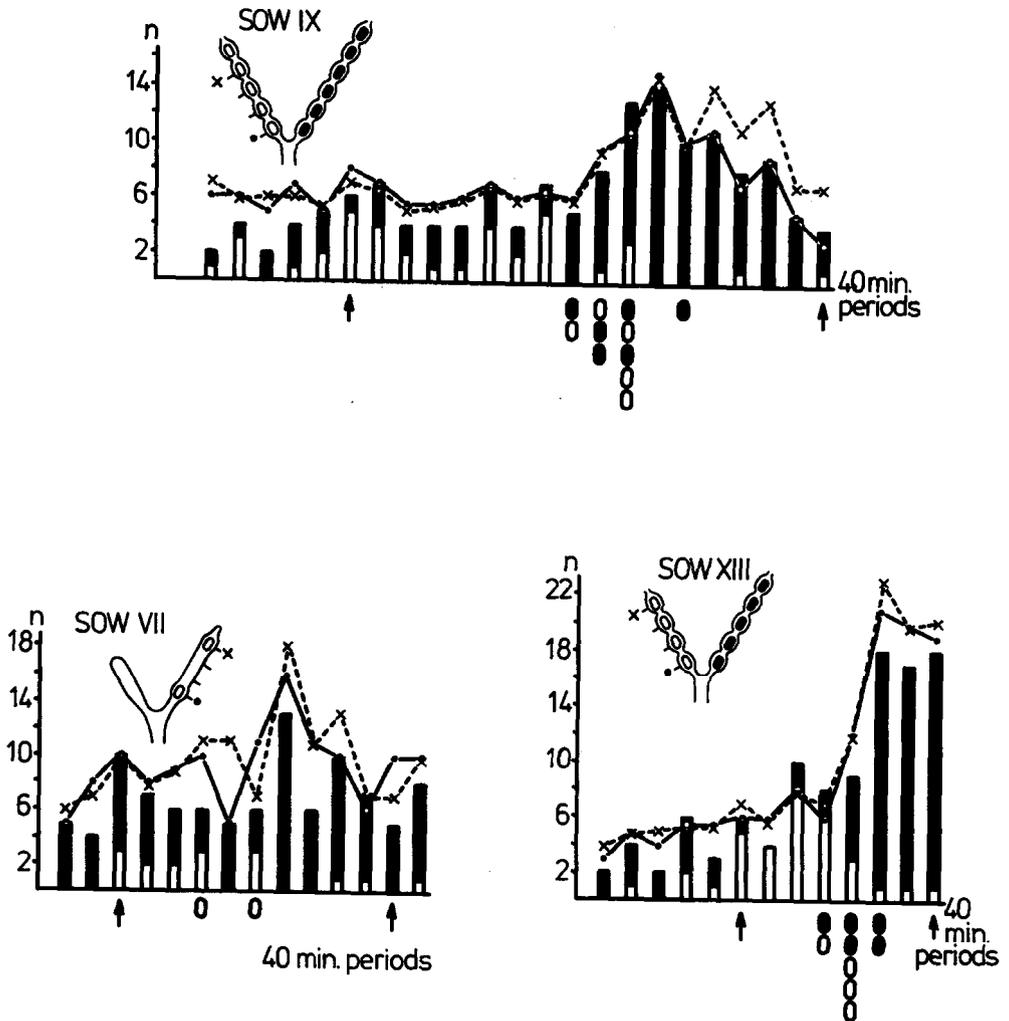


Fig. 4. The frequency (per 40 minutes) of electrical activity phases recorded at the two most distant electrodes during parturition in three sows. The height of the vertical bars indicate the frequency of those phases that were propagated between 3 or 4 electrodes in either a tubocervical (black areas) or cervicotubal direction (white areas). The arrows on the left indicate the onset of straining, those in the right the delivery of the placentas. The diagrams give the relative position of the electrodes and the white and dark ovals represent expulsion of piglets from the horn with and without electrodes respectively.

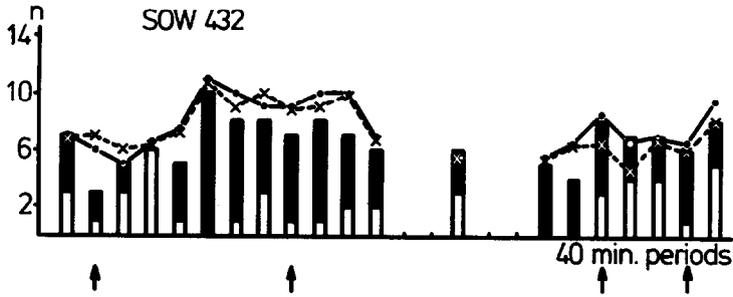


Fig. 5. The frequency (per 40 minutes) of electrical activity phases recorded at the two most distant electrodes (X - - - X EL 1; ● — ● EL 4, see fig. 6) during non-productive labour in sow 432. The height of the vertical bars indicate the number of phases that were propagated between 3 or 4 electrodes in either a tubocervical (black areas) or servicotubal (white areas) direction. Arrows on the left indicate the onset and stop of straining movements. Arrows on the right indicate the resumption of straining movements and the i.m. injection of 3 I.U. oxytocin (Syntocinon, Sandoz, Basel, Switzerland).

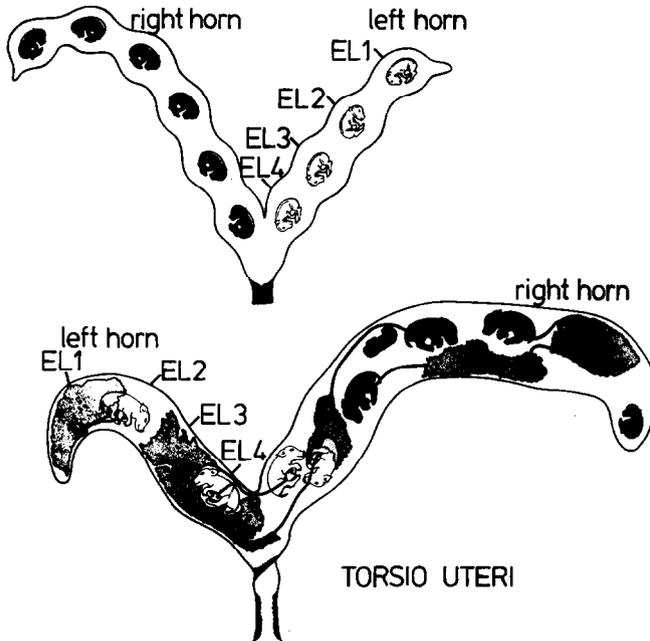


Fig. 6. Intrauterine location of fetuses in sow 432 as observed during laparotomy on D83 of gestation (upper part) and at autopsy on D115 (lower part) after about 48 hours of non-productive labour. Four electrodes (EL 1, 2, 3 and 4) had been implanted on the left horn (see text).

is given by the black and open parts respectively. The following conclusions can be derived from this figure:

- in all three sows the frequencies measured at the two electrodes were almost similar with only two exceptions: the frequency at the most cervically implanted electrode in sow nr. VII decreased shortly after expulsion of the first (mummified) fetus beneath it and in sow nr. IX a prolonged discrepancy between the two frequencies after expulsion of the last piglet was caused by a number of extinguished tubocervically directed phases that did not reach the most cervically implanted electrode.
 - from the onset of straining until the end of parturition 54-100% of all phases within a 40 minutes period were propagated between 3 or 4 electrodes. In cases where the number of propagated phases exceeded the frequencies at the two electrodes "echo-propagation" occurred.
 - cervicotubally directed activity phases occurred in all three animals and were even dominant during several 40 minutes periods in sows IX and XIII. The same was true in the (not shown) animal that aborted. The cervicotubally directed phases decreased in number or even completely vanished after delivery of the piglets from the horn with electrodes. During expulsion of the remaining piglets from the other horn and the placentas the phases were almost exclusively propagated in a tubocervical direction.
- Both types of propagation as well as "echo-propagation" also occurred during labour in the animal with a uterine torsion (Fig. 5). By contrast their relative distribution continued to fluctuate during 24 periods of 40 minutes without a permanent change. At autopsy at D115 (i.e. 12 hours after the last 40 minutes period of Fig. 5) an 180° precervical uterine torsion was found, apparently caused by incorrect replacement of the two uterine horns after fetal marking and electrode implantation on D83. The intra-uterine locations of the (dead) fetuses at autopsy as compared with those established during surgery are illustrated by Fig. 6. Only two piglets from the horn with electrodes were still in more or less the same position; the other two piglets from this horn had passed the uterine body and were located in the other horn. Piglets from this latter horn had mixed up. Two fetuses were mummified.
- the frequencies of the activity phases reached maximal values during the first 40 minutes period after completion of expulsion from the horn with electrodes (Fig. 4).

After emptying of the horn a sustained and significant reduction of the mean duration of the activity phases was established despite the large variations measured before as well as after this time (Table 2; compare figures 3 and 8). Similar and synchronic changes in the duration of the activity phases were measured from all electrodes.

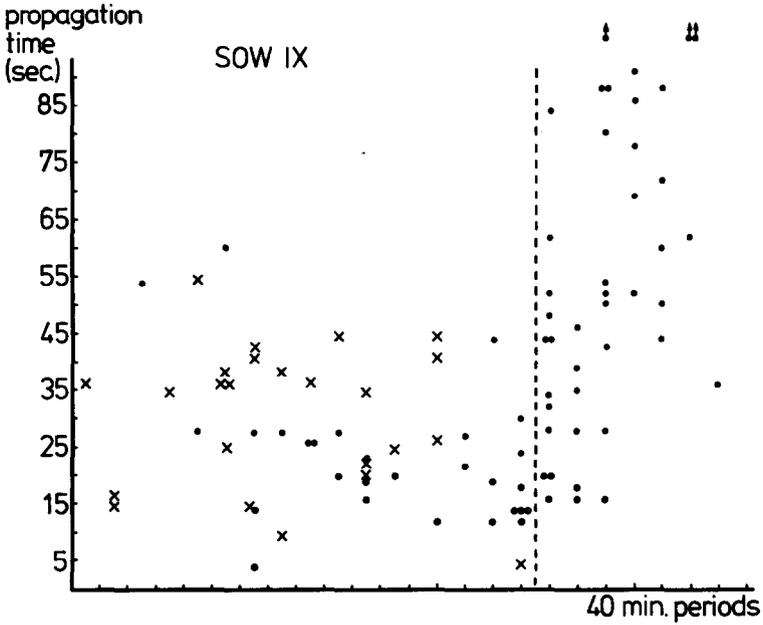


Fig. 7. Propagation-time (sec) of phases of electrical activity between the two most distally implanted electrodes in sow IX (see diagram fig. 4). The dotted vertical line indicate the completion of delivery of piglets from the horn with electrodes. (● tubocervically, X cervicotubally directed).

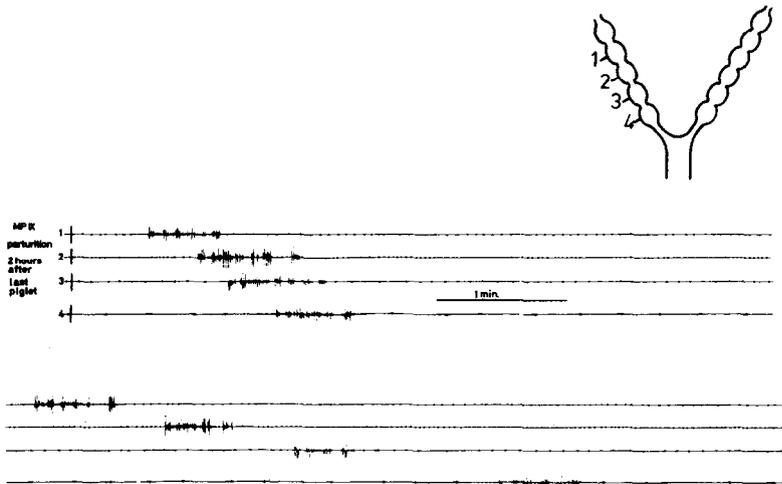


Fig. 8. Uterine electromyograph in two continuous sections from sow IX at two hours after expulsion of the last piglet. Two successive phases are both propagated in a tubocervically direction but with a much different propagation-time.

TABLE 2

The mean duration (sec, \pm SD) of myometrial electrical activity phases during two hours before and after completion of expulsion of piglets from the horn with implanted electrodes. Measurements in all sows are from an electrode overlying the most cervically located piglet, which in sows VII and 403 turned out to be mummified fetuses.

sow nr	mean duration of activity phases (sec)		
	horn pregnant	horn empty	
MP III	125 \pm 46 (n=18)	79 \pm 31 (n=27)	*
MP VII	66 \pm 28 (n=27)	48 \pm 11 (n=37)	*
MP IX	122 \pm 53 (n=27)	53 \pm 27 (n=35)	*
MP XIII	157 \pm 68 (n=24)	65 \pm 32 (n=59)	*
MP XIV	104 \pm 48 (n=33)	63 \pm 21 (n=35)	*
MP 403	63 \pm 21 (n=46)	40 \pm 8 (n=23)	*

* $p < 0.005$, Wilcoxon test.

This shortening occurred rather abrupt so that in the last animals of the experiment the completion of expulsion from the horn with electrodes could be predicted without even knowing the marked sites of the delivered piglets.

Figure 7 illustrates the conduction-time between the most distant electrodes in sow IX for all activity phases that were propagated in either a tubocervical or cervicotubal direction. Until completion of expulsion from the horn the mean conduction-time of the tubocervically directed phases (23.5 sec, SD \pm 12.3, n=28) was significantly shorter ($t=1.94$) than the mean conduction-time of the cervicotubally directed ones (30.3 sec, SD \pm 12.7, n=24). The same was found in sow 432 (with uterine torsion) but the reverse was true for sow XIII. No significant difference was found in sow VII.

After completion of expulsion from the horn with electrodes the conduction-time increased (Figure 7, sow IX): values from 80 minutes after completion of expulsion being significantly greater ($0.01 < p < 0.025$) than those during the first 80 minutes. The same was true in sow VII and XIII. However, the most striking feature was the great variation of the conduction-time of activity phases during parturition, even of two successive ones (Fig. 8).

DISCUSSION

This study demonstrated the presence of synchronic and well propagated electrical activity in the uterus of the sow during parturition. Similar findings, obtained with comparable techniques, have been reported from the parturient rabbit (Kao, 1959; Csapo et al., 1963; Naaktgeboren et al., 1975) and rat

(de Paiva and Csapo, 1973). Like in these last two species (Melton and Saldivar, 1964; Porter, 1975) electrical activity may spontaneously start at any point along the uterine horn of the sow. Because of this one can never be sure with in vivo studies that the recorded electrical activity at one electrode represents propagated activity from another. However, the synchrony of both activity phases and intervals of inactivity (1-5 minutes) strongly suggests that the successive appearance of electrical discharges at successively implanted electrodes represents propagated activity.

The changes in origin, mean duration and mean propagation-time of the activity phases upon spontaneous delivery of the fetuses from the horn with electrodes indicate that the presence of fetuses within a uterine horn determines the characteristics of its muscular activity. A similar conclusion was based on electromyographs made during late pregnancy where the uterine segments, overlaying a fetus showed more spontaneous electrical discharges than empty parts of the horn (Taverne et al., in preparation). That uterine volume is one of the important regulatory factors of myometrial activity was concluded by Csapo et al. (1963) who recorded similar changes in myometrial electrical activity from the rabbit uterus by changing the volume experimentally after manual removal of the fetuses.

A local effect of mechanical stimulation of one uterine horn has been clearly demonstrated by Cross (1958) in the rabbit and by Rousseau and Prud'homme (1976) in the sheep: the absence of any change in the contralateral horn excluded a central nervous or neurohumoral pathway of excitation. By contrast, a mutual relation between uterine contractions of the two uterine horns has been observed by cinematography in the post partum rabbit (Naaktgeboren and Carter, 1971) and rat (Schoof and Naaktgeboren, 1975): tubocervically directed contractions of one horn occasionally proceeded as cervicotubally directed ones in the contralateral horn. Uterine electromyographs from pregnant sows and non-pregnant sheep with electrodes on both horns and the uterine body indicated that the same may be true in these latter two species (Taverne, unpublished data). So at least some of the cervicotubally directed activity phases that have been recorded during delivery may be continuations of tubocervically directed ones from the other horn. The same can be said for those echo-propagated phases that changed their direction at the most cervically implanted electrode. However, the change in direction of echoed phases was also recorded at the tubal end of the horn and spontaneous reverberations of electrical activity have been recorded in vitro from uterine strips of oestrogen-treated ovariectomized rats (Melton and Saldivar, 1964).

While after completion of delivery the distances between the electrodes can be expected to be shorter by retraction of the uterine musculature, the mean

conduction-time of the activity phases between the electrodes significantly increased. In addition the great variation of individual propagation-times that were measured both before and after delivery remains puzzling. Gap-junctions between myometrial cells probably underlie the myogenic propagation of electrical activity in the uterus and in the rat their formation seems to be essential in the process of initiation of parturition (Garfield et al., 1978). If the same is true in the sow, one must postulate an unequal distribution of gap-junctions between bundles of myometrial cells to explain the large differences in propagation-time of even two successive activity phases. Specialized pathways of propagation within a uterine horn have already been postulated for the rat by Melton and Saldivar (1964). Another explanation could be a pulsatile release of oxytocin. This hormone facilitates propagation (Marshall, 1974) and in successively taken, integrated 2-minute blood-samples of some of our parturient sows rather fluctuating levels of oxytocin have been found (Forsling et al., 1979).

The differences between the mean propagation-time of cervicotubally and tubocervically directed activity phases are not uniform in character and more data are needed. However, cervicotubally directed impulses have been found to be propagated at a greater velocity in the myometrium of the pregnant mouse (Goto et al., 1959) and oestrous ewe (Prud'homme, 1976) and this seems to implicate that propagation-time is determined also by intrinsic myometrial factors.

At this time one may only speculate on the functional importance of cervicotubally directed contractions before and during expulsion of the fetuses. During the course of labour the uterine horn will be transformed into a slippery tube by rupturing of the ends of the chorionic sacs, while the individual placental connections stay in tact (Perry, 1954; Ashdown and Marrable, 1970). In such conditions piglets can be moved in either direction of the horn, the length of their umbilical cords and the placental connections being limiting factors. Depending on the temporary presence or absence of a fetus, uterine segments may contract isometrically or isotonicity. Tubocervically directed contractions can propel a fetus in the same direction only as long as the uterine segment between that fetus and the pelvic inlet remains flaccid. As soon as this segment also contracts the piglet will be enclosed by two isotonicity contracted uterine parts. When one of the most caudally positioned fetuses has approached the pelvic region (which seems to occur by chance from one of the two horns according to Dziuk and Harmon (1969) and Taverne et al. (1977)), its presence may initiate there a cervicotubally directed contraction. This contraction would prevent a slip-back of this fetus into the uterine horn and would cause a transport of the other fetuses in a cervicotubal direction. An intact umbilical and

placental circulation of the more tubally located piglets can be safeguarded in this way as long as possible. Despite a considerable retraction of the uterine wall of the already emptied parts of the horn, as can be easily observed during caesarean sections, the last piglets will have to be transported over a longer distance than the first fetuses. This may explain the higher number of broken umbilical cords and dead born piglets during the last part of delivery (Randall, 1972).

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