Electrical and mechanical activity of the cervix in the ewe during pregnancy and parturition

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Summary. Myoelectrical and mechanical activities of the uterine cervix and horns of ewes fitted with electrodes and strain gauges were measured from the 30th day before until the 3rd day after parturition. During pregnancy, cervical electromyograms presented regular episodes of strong activity of a mean duration of 7 min, termed regular spiking activity, occurring at about 50-min intervals. Between two episodes, isolated or low frequency spikes occurred randomly and constituted the irregular spiking activity. The alternation of irregular and regular spiking activities was called the myoelectrical complex of the cervix. Clear relationships were noticed between electrical and mechanical events. On the pregnant uterine horn (singleton pregnancy) or on both horns (twin pregnancy), a myoelectrical complex pattern similar to that of the cervix was recorded. Regular spiking activity on the cervix and pregnant horn(s) occurred mainly simultaneously.

No significant evolution of the myoelectrical complex pattern was noted throughout the last month of pregnancy until 2–3 days before parturition. The activity pattern was then modified according to three characteristic phases: (1) a phase of relative inhibition of the cervix and pregnant horn(s) 48 h before lambing and lasting about 17 h; (2) a phase of increasing activity occurring thereafter over the whole genital tract with an average duration of 31 h; and (3) a phase of continuous activity of the cervix and uterus for 0.4–3.8 h which accomplished the expulsion of the lamb.

It is concluded that during the last month of pregnancy the cervix is active and that its activity arises from a basic ultradian rhythm involving the entire genital tract. Furthermore, although our results do not offer an explanation for the preparturient increase of cervical compliance described by others, they definitely excluded cervical muscular inhibition during the last 24 h of pregnancy and at the time of cervical dilatation.

Introduction

Uterine activity in sheep during pregnancy and around parturition has been extensively described (Hindson, Schofield & Turner, 1968; Naakteboren *et al.*, 1975; Prud'homme & Bosc, 1977; Krishnamurti, Kitts, Kitts & Tompkins, 1982; Harding *et al.*, 1982). In contrast, the possibility of motor activity of the cervix during pregnancy has not been evaluated. There may be several reasons to explain this lack of investigation. The pressure techniques which have been extensively used to assess uterine motility during pregnancy and parturition are not entirely appropriate to evaluate the spontaneous motility of the cervix since the presence of a device within this portion of the genital

tract could interfere with its spontaneous motility (Stys, Clewell & Meshia, 1978) and would be expelled by the progression of the conceptus. Moreover, the cervix in sheep throughout most of the pregnancy has been described as a closed and collagenous tube (Fitzpatrick & Dobson, 1979) and thus considered to be a mechanically inactive organ. In fact, the cervix musculature is well developed in sheep (Raynaud, 1973) and may be active during pregnancy, as shown in non-pregnant ewes (Garcia-Villar, Toutain, Moré & Ruckebusch, 1982b).

Before parturition, comprehensive studies have shown that major alterations of stretchability (compliance) and diameter (dilatation) must occur to permit the expulsion of the conceptus (Fitzpatrick, 1977; Stys *et al.*, 1978; Fitzpatrick & Dobson, 1979). Compliance increases over a few hours before parturition and decreases rapidly after birth. No adequate explanation is yet available to specify the mechanism involved in such rapid variations in compliance. A possible role for cervical muscle (inhibition or contraction) has never been considered, although Stys *et al.* (1978) reported a gradual decrease in cervical mechanical activity with the approach of parturition.

The aim of the present work was (1) to describe the spontaneous electrical and mechanical activities of the ovine cervix from the 30th day before until the 3rd day after lambing, and (2) to investigate the possible relationships between cervical and uterine motility.

Materials and Methods

Nine ewes of mixed breeding and of known gestational age, weighing 53–61 kg, were used. Seven ewes which underwent surgery between the 81st and the 106th days of pregnancy were used for the analysis of the pregnancy period, i.e. from the 30th until the 4th day before lambing. One of these ewes was disregarded for the analysis of the peripartum period, i.e. from the 3rd day before until the 3rd day after lambing, while 2 other ewes, subjected to surgery 12 and 18 days before parturition were also considered.

Surgical and recording procedures were as described in detail by Garcia-Villar *et al.* (1982b). Two groups of intraparietal electrodes were placed on the ventral cervix. Three other groups were placed on each uterine horn (gravid and sterile) near the uterotubal junction, the middle and the base of the horns. In addition, in 5 ewes, three strain gauges were placed near the middle group of electrodes on each horn and on the ventral cervix between the two groups of cervical electrodes.

Throughout the experimental period, animals were kept in individual cages. The electrodes and the gauges (when present) were continuously connected to the input panel of the amplifiers. 'Direct' records were performed 4–8 h per day until 3–4 days before parturition and were then obtained continuously (24 h per day) at a paper speed of 0.5 to 20 cm per min, until 3 days *post partum*. In addition, 'integrated' records (Latour, 1973) were obtained continuously (24 h per day) throughout the experimental period at a paper speed of 6 cm per hour, as a monitoring procedure.

All ewes exhibited normal pregnancy (145.3 ± 2.33 (s.d.) days) and parturition, producing healthy active lambs with only one set of twins.

Results

Activity profile during the last month of pregnancy

Elementary electromyographic signals and related mechanical activity. These characteristics recorded for the cervix of the pregnant ewe were the same as those described formerly for cyclic and ovariectomized ewes (Garcia-Villar *et al.*, 1982b), i.e. short spikes of < 0.25 sec in duration and of high amplitude ranging from 200 to 600 μ V and long spike bursts of 20–80 sec in duration and of low amplitude (20 to 60 μ V). Short spikes were recorded in all of the ewes whatever the day of pregnancy or the location of the electrodes on the cervical wall. In contrast, long spike bursts were seen occasionally in 3 of the 7 ewes.

Each of these two basic signals was closely related to changes in mechanical activity as recorded with strain gauge transducers. Isolated short spikes elicited individual elevations of the base line for a few seconds, while a sustained rise was observed when short spikes occurred at a high frequency. Long spike bursts gave sustained elevations of the base line (Text-fig. 1a). Consequently, subsequent use of the term 'activity' will refer to the electrical and mechanical events, although most of our data refer to electrical rather than mechanical measurements.

Text-fig. 1. Electromyogram (2) and related mechanogram (1) of the ovine cervix (a) and pregnant uterine horn (b). In (a) short spikes of high amplitude occurring in series (upper traces) and long spike bursts of low amplitude (lower traces) elicit sustained increase of the mechanogram baseline. Both types of activity can be recorded simultaneously at the same electrode and strain gauge sites. In (b) only one type of electrical signal is recorded in the uterus mainly in the form of a series of bursts of spikes of high amplitude corresponding to a marked mechanical activity.

Occurrence of cervical activity. The spiking activity (short spikes) of the cervix did not occur randomly but followed a typical pattern (Text-fig. 2). As in cyclic and ovariectomized ewes, a periodic and sustained spiking activity, which was the main feature of the cervical electromyogram, was termed regular spiking activity of the cervix. This activity consisted of a series of short spikes (Text-fig. 2) with a frequency range of 10–33 (Table 1). The duration of each episode of regular spiking activity was evaluated for each ewe and each day (Table 1). No significant differences were observed throughout the last month of gestation for these two measurements (Duncan's multiple range test, $P > 0.05$).

Table 1. Characteristics of cervical electromyographic activity in the ewe during the last 30 days of gestation

Ewe	No. of myoelectrical complexes analysed	Regular activity		Irregular activity	
		Duration (min)	Frequency of short spikes (min ⁻¹)	Duration (min)	Frequency of short spikes (min ⁻¹)
01	224	5.85 ± 0.397	12.7 ± 3.88	31.3 ± 12.93	2.87 ± 1.29
06	179	7.7 ± 1.87	16.3 ± 4.32	26.2 ± 6.71	1.87 ± 1.35
49	190	9.3 ± 1.279	10.6 ± 3.37	45.5 ± 12.87	0.976 ± 0.502
53	183	7.4 ± 0.85	32.9 ± 7	46.0 ± 9.26	1.18 ± 1.02
72	202	6.7 ± 1.34	17.5 ± 3.18	51.2 ± 27.84	0.4 ± 0.31
21	198	5.3 ± 1.526	16.0 ± 6.12	42.2 ± 25.92	0.96 ± 0.343
22	182	6.4 ± 1.39	19.2 ± 4.25	68.2 ± 50.08	1.02 ± 0.94
	Total	6.97 ± 1.34	17.87 ± 7.22	45.78 ± 12.54	1.32 ± 0.805

Values are mean ± s.d.

Between each regular spiking activity, short spikes occurred randomly with a low frequency (0–5 per min) and the interval between two regular activities was therefore one of irregular spiking activity. The duration of irregular spiking activity, evaluated for each sheep and each day, is presented in Table 1. There were no differences within the last month of pregnancy (Duncan’s multiple range test, *P* > 0.05). As in cyclic and ovariectomized ewes, the alternation of irregular and regular activities was called the myoelectrical complex of the cervix.

In addition to this complex a second rhythm of activity was recorded with the same electrodes but only for 3 out of the 7 ewes, and then not consistently: long spike bursts occurred with a frequency of 14–30/h (Text-fig. 2).

Text-fig. 2. Activity pattern of the pregnant horn (P), the non-pregnant horn (NP) and cervix (CX) in a singleton pregnancy (integrated electromyogram). The cervix and pregnant horn display synchronously a strong periodic activity termed regular spiking activity (RSA). Long spike bursts (LSB) of low amplitude were also present, but only on the cervix. In contrast, the sterile horn has weak or no activity.

Activity of the cervix during the last month of pregnancy. The development of cervical activity during the last month of gestation was evaluated by counting the total number of regular spiking activities (Text-fig. 3). The correlation coefficient between the mean frequency per day and time before parturition ($r = 0.03$) was not significant, indicating absence of change throughout the last month of gestation. The mean $\pm$ s.d. 24-h value for all sheep and all days was 28.5 ± 3.71 .

Text-fig. 3. Number of regular spiking activities (RSA) per day on the ovine cervix. No significant changes were observed throughout the last month of pregnancy, but diurnal values (from 8 to 20 h) were slightly but significantly lower than nocturnal values (from 20 h to 8 h) (paired t test; $P < 0.01$).

Uterine activity. From the pregnant uterine horn (singleton pregnancy) or from both uterine horns (twin pregnancy), a recurrent pattern of activity was recorded throughout the period of investigation. This activity consisted of bursts of spikes of high amplitude (400–600 μ V), either intermingled or separated (4–8 sec duration; 4–6/min), which appeared in series and presented clear mechanical relationships (Text-fig. 1b). By analogy with the cervix, this activity was termed regular spiking activity of the uterus. In addition, isolated bursts of spikes occurred randomly from the pregnant horn between two episodes of regular spiking activity. The alteration of irregular and regular activities constituted a myoelectrical complex. The mean $\pm$ s.d. duration of regular spiking activity for the 7 sheep was 8.19 ± 1.10 min and was significantly longer than the mean duration of the regular activity of the cervix ($P < 0.01$; paired t test). As for the cervix the mean duration of episodes of regular spiking activity did not change throughout the last month of pregnancy.

In contrast to the gravid horn, the activity of the empty horn was weak or nearly absent. When present, the activity consisted of regular spiking activity of low amplitude (100 μ V) occurring synchronously with that of the gravid horn.

Relationships between uterine and cervical activities. The regular spiking activity of the gravid horns and of the cervix was nearly always synchronous, although there was sometimes a short delay (30–90 sec) between the activation of the two structures. To identify a possible pace-maker area, the spread of the activation of the 1358 analysed regular spiking activities was evaluated. It appeared that activation began in the cervix in 25.3% of cases, in the gravid uterine horn in 36.2% and both simultaneously in the remainder. Thus no preferential spread of activation can be specified.

Activity profile around parturition

Dramatic changes in cervical activity were observed within the 2–3 days before lambing, when compared to the 'control' period between the 8th and the 4th day before parturition (Text-fig. 4a).

Table 2. Characteristics of the episodes of regular spiking activity in the cervix of the ewe before parturition

	'Control' period† (N = 8)	Inhibitory phase (N = 7)	Phase of increasing activity (N = 8)
Frequency of occurrence (h ⁻¹)	1.48 ± 0.96	0.91 ± 0.66**	3.24 ± 1.06***
Duration (min)	7.1 ± 1.64	6.3 ± 0.89*	5.1 ± 0.94*
Frequency of spikes within each episode (min ⁻¹)	20.1 ± 7.43	16.9 ± 5.24*	18.2 ± 7.11

Values are mean ± s.d. for the no. of sheep indicated.

† Days -8 to -4 before lambing.

Significantly different from the control values (paired *t* test): *P < 0.05; **P < 0.01; ***P < 0.001.

The first event heralding the imminence of parturition was a significant decrease in cervical activity. This inhibition, clearly observed in 7 out of the 8 sheep (Table 2), occurred 48.9 ± 11.17 h (range 33–69 h) before parturition and lasted 17.4 ± 4.99 h (range 12–22 h). During this inhibitory phase, the frequency of occurrence of regular spiking activity was significantly reduced (Table 2). The duration of each episode and the frequency of spikes within each episode of regular activity were also significantly decreased. A drop of 54% of the total number of spikes per hour was observed in the 7 sheep which displayed an inhibitory phase. When present, the long spike bursts recurred regularly at about 2–4-min intervals. After the inhibitory phase, cervical activity returned to its previous level and subsequently increased progressively (Table 2). During this second phase, which occurred 31.4 ± 11.11 h (range 23–55 h) before parturition and lasted 29.6 ± 10.77 h (range 19.5–53 h), cervical activity continued to display a regular spiking activity pattern but with a significantly higher frequency than during the control period (Table 2). In addition, the irregular activity became progressively more important; the total number of short spikes per hour during this phase was 320% higher than during the control period. The enhancement of the occurrence of irregular spiking activity led to continuous high levels of activity in the cervix and it became impossible to separate regular from irregular spiking activities. During this third phase, lasting 1.81 ± 1.10 h (range 0.4–3.8 h), the expulsion of the lamb(s) was achieved (Text-figs 4 & 5).

Activity of the cervix after parturition. During the first 2–6 h after parturition, the cervix continued to display a high level of activity; it presented mainly short spikes occurring continuously with a high frequency. Thereafter, cervical activity decreased progressively to become very weak within 48–72 h. During these 3 days *post partum*, the typical pattern of cervical activity which had been recorded during pregnancy and before parturition was never observed.

Uterine activity around parturition. As for the cervix, a distinct inhibitory phase was observed on the gravid horn, starting 43.3 ± 11.27 h (mean ± s.d.) before parturition, but this value was not significantly different from that of the cervix for the 8 sheep. During this first phase, there was a dramatic decrease in the number of regular spiking activities per hour when compared to the control period (0.71 ± 0.31 and 1.48 ± 0.96 respectively) (mean ± s.d.; *P* < 0.01; paired *t* test) and the duration of the episodes of regular spiking activity was significantly reduced (6.1 ± 1.85 and 8.0 ± 1.28 min) (mean ± s.d.; *P* < 0.001; paired *t* test). In 7 out of the 8 ewes this inhibitory phase began between 17:00 and 20:00 h. After the inhibitory phase, the activity of the gravid horn returned to its previous level while the empty horn, which was formerly silent or had weak activity, began to display a regular spiking activity pattern. The occurrence of irregular spiking activity progressively increased between the episodes of regular spiking activity and this led to continuous activity during the expulsion of the conceptus. After parturition, uterine activity was similar to that described by others.

Text-fig. 4. Electromyogram and related mechanogram of pregnant horn (P), non-pregnant horn (NP) and cervix (CX) before (a) and during (b) the expulsion of the lamb (arrow). In (a) the phase of increasing activity (12 h before lambing) is shown, while (b) shows the phase of continuous activity (lambing).

Relationships between uterine and cervical activity around parturition. During the control period, the episodes of regular spiking activity occurred synchronously over the whole genital tract. Thereafter, the three phases which were distinguished, i.e. inhibitory phase, phase of increasing activity and phase of continuous activity, occurred nearly simultaneously in the two structures, though sometimes episodes of regular spiking activity were present only on the cervix. As during pregnancy, no preferential spread of activation was observed within the 3 days before parturition. In contrast, just after the expulsion of the lamb preferential propagation of contractions occurred from the uterus towards the cervix. Thereafter, a progressive dissociation of activity was observed and the activity then occurred randomly over the entire genital tract.

Text-fig. 5. Activity pattern of the pregnant horn (P), non-pregnant horn (NP) and cervix (CX) around parturition in a singleton pregnancy (integrated electromyogram). (a) The activity pattern of pregnancy (-72 h) was modified by a phase of relative inhibition (-36 h) followed by a phase of increasing activity and then involving the entire genital tract (-18 h). (b) The enhancement of irregular activity led to a more or less continuous pattern of activity which accomplished the expulsion of the lamb (arrow). A high level activity was recorded during 2–3 days *post partum* but activity then declined progressively in the entire genital tract.

Discussion

The results of the present study, using suitable techniques for long-term recording from the cervix (Garcia-Villar, Toutain & Ruckebusch, 1982a), contrast with the view of a quiescent cervix during pregnancy, since a typical pattern of activity in the cervix was recorded during the last month of pregnancy and around parturition. In addition, the clear temporal relationships between the activity of the cervix and the pregnant horn(s) suggest that the uterus and cervix must be viewed as a whole.

In the cervix, elementary electromyographic signals and associated mechanical activity were similar to those recorded in cyclic or ovariectomized ewes (Garcia-Villar *et al.*, 1982b). Similarly, the major electrical signal, i.e. short spikes, was organized in the so-called myoelectrical complexes, recurring approximately every 50 min. The present study shows the nearly synchronous appearance of regular activity in the cervix and the uterus. Such a pattern of periodic activity has been described for the uterus of the pregnant ewe by many authors using different terminology such as “train of action potentials” (Krishnamurti, Kitts & Tompkins, 1979); “bursts” (Harding *et al.*, 1982); and “periods or bursts of activity” (Bontekoë, Blacquièrè, Naakteboren, Dieleman & Willems, 1977). No preferential spread of activation between the uterus and cervix has been demonstrated, in agreement with Harding *et al.* (1982) who have shown that activity appears synchronously at several sites in the uterus, suggesting humoral control or diffuse stimulation by a nerve network.

The origin and meaning of the synchronous regular activity of the cervix and uterus remain unclear. This latter is not specific to pregnancy nor is it restricted to a particular location of the ovine genital tract. Such a synchronous regular activity has been described in the uterus and the oviduct during oestrus (Ruckebusch & Buéno, 1976), in the uterus and the cervix during oestrus and after oestrogenic treatment of ovariectomized ewes (Garcia-Villar *et al.*, 1982b) and in the cervix during the luteal phase, after ovariectomy and during seasonal anoestrus (Garcia-Villar *et al.*, 1982b; and unpublished observation). Consequently, we suggest that the entire genital tract of the sheep (oviduct, uterus and cervix) displays a synchronous ultradian rhythm which may exist in the absence of oestrogen (cervix) or after oestrogen priming (oviduct and uterus). In this respect, although plasma oestrogen concentrations remain < 40 pg/ml until parturition in sheep (Challis *et al.*, 1979), myometrial concentrations > 1200 pg/g have been measured between Days 100 and 115 of gestation (Rawlings & Ward, 1976). Such a high local concentration is probably due to local transport from the feto-placental unit and may explain the occurrence of activity at the uterine level, which has been observed in ewes as early as the 5th week of pregnancy (Van der Weyden, Taverne, Dieleman & Fontijne, 1981) and which is higher in the pregnant horn than in the sterile horn (present study).

The second part of the present study describes the development of cervical activity within the period which includes two major events that contribute to parturition, i.e. softening of cervical tissue and dilatation. Both events must be clearly distinguished (Hollingsworth & Gallimore, 1981): the former is a progressive change in the tensile properties of the cervical wall while the latter is an increase in diameter which allows the conceptus to be expelled. In sheep, softening of the cervix has been evaluated *in vivo* by means of cervical compliance measurements. Several authors report that cervical compliance increases during uterine quiescence (Fitzpatrick, 1977; Fitzpatrick & Dobson, 1979) and more precisely within 12 h before the onset of uterine activity characteristic of labour (Stys *et al.*, 1978). Consequently, it can be suggested that the increase of cervical compliance begins during the phase of relative inhibition of the motor pattern of pregnancy reported in the present paper. This phase, occurring 2 days before parturition and lasting about 17 h, has not been described previously. It has also been demonstrated that porcine relaxin is able to inhibit myometrial activity in sheep as in other species (Porter, Lye, Bradshaw & Kendall, 1981) and that administration of exogenous relaxin induces cervical softening in ruminants (Perezgrovas & Anderson, 1982). At the present time, it has not been reported that cervical softening in sheep coincides with an increasing peripheral blood concentration of relaxin. However, the occurrence of an inhibitory phase of activity in the cervix and uterus at the presumed time of the beginning of cervical softening supports the hypothesis of relaxin secretion about 48 h before parturition.

After the inhibitory phase, the uterus and cervix showed dramatic increases in activity which led to continuous activity during the expulsion of the conceptus. The phase of increasing activity, lasting about 30 h, seems to be without effect on the expulsion of the conceptus despite the supposed high compliance of the cervix.

The final dilatation of the cervix, i.e. the increase in diameter, must have occurred only during the phase of continuous activity. Cervical dilatation might be a passive phenomenon due to the distension of a soft structure by the progression of the conceptus during this phase of strong uterine activity and concomitant abdominal contractions. However, the possibility of cervical muscular relaxation can be totally excluded as a result of our studies. On the contrary, cervical muscular activity may contribute to the expulsion of the conceptus. After parturition, the whole genital tract continues to display a high level activity for 2–6 h, propagated mainly from the uterus towards the cervix. Thus, it can be suggested that, even though a pressure gradient is sufficient to expel the lamb, co-ordinated propagated waves are probably more effective for expulsion of the placenta. Thereafter, the activity of the entire genital tract progressively declines, as has been shown for the uterus by many authors.

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