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THE ELECTRICAL ACTIVITY OF THE
PREGNANT SHEEP'S UTERUS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

by


The Ohio State University
1964

Approved by

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Department of Veterinary Physiology
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Figure pages are not original copy.
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best way possible.

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intrauterine pressure and calculated some of the standard
deviations. Mr. Steven Boggs assisted with many of the
technical problems, and Mr. Satvin Kramer made most of the
illustrations. Dr. Richard Ray made the photographs of the
uterus during surgery. Many students contributed to this
work, some a very significant amount. To all of these
people and to the many others goes my deepest gratitude.
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If the complete list of persons directly or indirectly responsible for this work were published it would require far too much space. In lieu of such a list some individuals must be mentioned specifically.

Dr. J. R. Smith, a scholar and teacher in the finest sense of the word, has assisted in the development of many graduate students who demand much but give little. He has given most generously of his time and advice in the furtherance of this project and my education.

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Dr. D. R. Whitney and the staff of the numerical computation laboratory set up the calculations for
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INTRODUCTION

The mechanism of parturition has been investigated in many different ways. The problem has been approached from the cellular standpoint, the flow of ions in and out of the cell, or the electrical activity of individual cells; from the endocrinological principles, the effects of the placenta, the level of hormones in body fluids, or the effects of hormones on parturition. Small pieces of the myometrium have been used for electrical or mechanical studies. Many techniques have been applied to humans, but of necessity this work has often been limited to certain rather crude techniques. From these investigations has come our knowledge concerning the process of parturition, but what of the behavior of the whole organ, in place, in the animal body? Studies of intrauterine pressure have given some knowledge of the results of activity by the whole organ. The question still remains of how this pressure develops, and how it changes as parturition approaches.

Some of the work has led to the theory of pacemakers in the myometrium, some say in a particular area or areas, others say pacemakers may be anywhere. Hence, does the uterus expel the fetus by peristaltic waves of contraction
driven by a pacemaker or pacemakers, or is the uterus like a balloon with one end open and all areas exerting equal force on the orifice.

Most of the work has been done on animals with placentas with the attachment over a localized area of the uterus. What of animals with a cotyledonary type placenta? The placental attachment is certainly no larger, but is rather evenly distributed over the whole myometrium. Very little has been done on the larger domestic animals and the cow and sheep are unique in this group since they have a cotyledonary type placenta.

The objects of this experiment have been to describe the electrical activity of the whole uterus prior to and during parturition under conditions as close to normal as possible. Specifically, (1) how much activity is present in various parts of the uterus; (2) is the activity regular; (3) does it start from one area and spread over the whole uterus; (4) is it usually initiated at any particular area; and (5) can the recorded electrical activity be correlated with the mechanical activity as reflected by contractions of small areas of the uterus and by the intrauterine pressure.
LITERATURE REVIEW

Electrical Activity Recorded

Directly from the Uterus

The earliest record of the electrical activity of the uterus was reported in 1910 by Theilhaber, cited by Falk and Nahon (36). One electrode was placed on the cervix and one in the rectum at the level of the fundus of the human uterus. There were curves which apparently were not cardiac or respiratory.

Blumenfeldt and Dahlman, cited by Falk and Nahon (36), recorded directly from the puerperal uterus of rabbits. There were electrical oscillations, but they were not associated with the mechanical movements of the uterus.

Greene (44) was apparently the first to describe a rapid series of spikes from the myometrium. He reported slightly diphasic, rhythmic, deflections of the galvanometer coincident with contractions of the uterus of the rat. The deflections occurred at a frequency of 117 to 120 per minute, with 25 to 36 deflections per series. He believed these were too fast to originate from the myometrium.
Voegtlin and De Eds (103) described slow changes in potential. These were highest just before contraction of the muscle and lowest at the peak, or just after the peak, of the contraction.

Hasama (48, 49) reported the appearance of slow diphasic waves of potential change in the virgin rabbit uterus. They occurred at a frequency of three to seven per minute and lasted approximately 12 seconds. These waves were related to the mechanical movement of the muscle, but the amplitude of the potentials had no relationship to the amplitude of the contractions. The potential changes increased in amplitude and frequency from the tubal to the vaginal end of the horn. The amplitudes from the longitudinal fibers were greater than those from the circular fibers.

Rosenblueth et al. (94) used the pregnant uterus from anesthetized or decerebrate cats. Stimulation of the hypogastric nerve resulted in the appearance of potential changes which were associated with contractions of the muscle. Spontaneous electrical activity consisting of a series of spikes or complexes was also associated with contraction.

Vazza, cited by Falk and Nahon (36), recorded the electrical activity of the uterus of rabbits in early
pregnancy. The electrical activity was made up of slow oscillations of potential which lasted 10 to 50 seconds. Each slow oscillation consisted of 10 to 20 smaller oscillations which occurred at a frequency of 20 to 100 per minute.

Falk and Mahon (36) used one large electrode on the fundus and one on the cervix. They recorded waves of potential change in various stages of the menstrual cycle of women. The average duration of the waves was 20 seconds.

Jacobson (52) was probably the first to record electrical activity directly from the human uterus in situ. He inserted needle electrodes through the cervix and plunged them into the myometrium. The subjects were nonpregnant and he attempted to relate his data to the normal menstrual cycle and to abnormalities of the menstrual cycle. The electrical activity consisted of bursts of spikes. The bursts were 2 to 20 seconds long and occurred at intervals of 4 to 14 seconds. Continuous electrical activity was noted in some subjects rather than bursts.

Balassa (5, 6) reported the absence of slow waves during late pregnancy in the rabbit and cat, but described spike potentials of 0.5 to 1.0 mv. (millivolts) occurring at a frequency of one to two per second in a series. The series were associated with vigorous spontaneous contractions. In
be tetanized. Monophasic spikes were obtained if one electrode was on an injured region of the strip and diphasic potentials if both electrodes were on an active region.

Bozler (12, 13) stated that the myometrium is a syncytium. He reasoned that it is a syncytium because (1) cocaine did not abolish the response; (2) the threshold was much higher when the stimulus was applied at right angles than when it was applied parallel to the long axis of the fibers, whereas, if conduction is due to a plexus of nerves it should make no difference if it is stimulated at right angles or on the long axis; (3) the characteristics of excitability, chronaxie, rate of conduction, and duration of the refractory period have a magnitude different from even the slowest nerve fiber; (4) the all or none relationship is valid; (5) electric currents have polar effects, whereas if all cells were units responding independently, all the cells between the electrodes would behave alike since they were subject to the same electric field; (6) the existence of injury potentials, which would not be expected from cells as small as those of the myometrium; and, (7) of the existence of action potentials. Therefore, he suggested that the uterus is a syncytium whose excitatory phenomena differs only quantitatively from nerve fibers.
early pregnancy or shortly after parturition there were both slow waves, at a frequency of 15 to 20 per minute, and the spike potentials.

Bozler (14) recorded "bursts" of spikes associated with spontaneous movement of uterine strips. The bursts lasted 4 to 60 seconds and the spikes occurred at 1.0 to 4.5 per second with a duration of 0.2 second. The duration of the bursts was greater in late pregnancy than in estrus.

This activity could be elicited by electrical stimulation, but the excitability was greatly decreased for 10 to 60 seconds following the previous burst. There were monophasic injury potentials when the muscle was injured 1 to 2 mm. from the lead.

Bozler (16) stated that since contraction of smooth muscle is accompanied by repetitive discharge the contraction can be considered tetanic.

Bozler (18) described three types of electrical activity in smooth muscle. He used strips of muscle from the estrus and pregnant uterus, ureter, and small intestine of the rabbit and cat. There were single brief spikes, repetitive discharge of the spikes, and long periods, up to 10 seconds, of sustained negativity. The uterus exhibited only the spikes and could be tetanized; but the ureter, which exhibited spikes and residual negativity, could not
Bozler (19) stated that the many functions of smooth muscle can be explained on the basis of classical muscle physiology if one considers that muscular excitability varies widely under different physiological conditions and that the nervous system can influence the excitability of visceral muscle through extrinsic nerves.

Tonus was defined as being a fluctuating level of tension or length on which brief contractions are superimposed. He noted that smooth muscle can maintain tension for long periods of time and that this can be shown to be the same as a twitch of skeletal muscle. It is only quantitatively different. It may be due to nonconducted potentials associated with weak contractions and to asynchronous activity in different parts of a muscle.

Woodbury and McIntyre (109, 110) were the first to use intracellular microelectrodes on the uterus. They used myometrium from pregnant humans, rabbits, guinea pigs, and cats. The resting potentials, depending on the species, averaged 27.0 mv. for the human to 44.7 mv. for the rabbit. Spontaneous action potentials were observed occasionally. They consisted of a peak with two spikes followed by a slow recovery. They had a magnitude of 2 mv., a duration of 0.2 second and recurred 1.3 times per second. They noted that the magnitude of the resting potential is low compared to that of skeletal muscle and theorized that this is the
Experimentally derived figures for chronaxie, rate of conduction and refractory period of the uterus of the guinea pig, rabbit, and cat were reported.

Bozler (15) summarized his thoughts on smooth muscle and classified it as follows:

- Many units
- Motor nerves

Skeletal

Multi-unit

Smooth muscle

Many units

Motor nerves

Multi-unit

Striated muscle

Syncytial automatic

Visceral

Cardiac

He stated that rhythmic activity in smooth muscle results from the coordinated activity of many muscle fibers which is not possible without some mechanism of conduction. Conduction may be blocked by areas of low excitability. Unstable excitability is characteristic of visceral smooth muscle. The great variability of the movements, characteristic of visceral smooth muscle, can be explained by the frequency of action potentials, number of impulses discharged, rate of conduction, and excitability.
result of a maintained, moderate increase in the permeability of the membrane to sodium rather than to impalement damage or a low potassium concentration gradient.

June (55) used decerebrate pregnant cats and recorded in situ from the uterus. He used unipolar leads. The electrodes were very fine silver wires attached to the uterus.

There were tetanic contractions of the uterus associated with a series of spikes. The length of the series was related to the duration of the contractions. The contraction was regular in various parts of the uterus, and was dependent upon conduction of stimuli over the organ. There appeared to be local pacemakers or automatic conductors which were responsible for continuous conduction of the contractions.

The duration of the series of spikes averaged between 17 and 24 seconds with extremes of 4 to 52 seconds. There was a 30- to 60-second interval between series which he believed due to the refractory period of the uterine muscle or of its local pacemaker. Prespikes occurred slightly before the beginning of a burst, or there were individual spikes, or rarely two in the interval between two bursts. The potentials in a series were 3 to 5 mv. in amplitude. The contractions occurred at an average of 30- to 50-second intervals.
Jung (57) attempted to relate the action potentials from the uterus to the strength of contractions. Decerebrate rats and cats were used. The electrodes were fine silver wire attached to the surface of the uterus. The indifferent electrode was placed, part of the time, on an injured portion of the uterus. Contractions were recorded simultaneously with the electrical activity.

The frequency of the action potentials seemed to be more related to amplitude of the contractions than was spike amplitude. Weak contractions had lower frequency. During a contraction the spike frequency would increase up to eight per second. Just prior to the peak of the contraction the frequency would begin to decline, and usually at peak contraction there were no spikes. He theorized that this decrease in the number of spikes at the end of a series indicated that the number of fibers stimulated also decreased. In summary, he believed that the spike frequency and the number of fibers activated were responsible for the strength of the contractions.

Jung (56) also investigated the origin and conduction of excitation in the uterus. He used decerebrate pregnant rats and cats and recorded with silver electrodes in situ. The reference electrode was placed on an inexcitable part of the animal's body. The electrical activity consisted of
a series of spikes which produced a true tetanus. The individual spikes had a duration of 0.2 to 0.3 seconds, but if a smaller wire was used, the duration was recorded as approximately 30 ms. (milliseconds). The frequency of the spikes varied slightly, being greater in the cat. Local potentials, or shallow oscillatory vibrations of potential occurred slightly before the first spike in a series. He concluded that these were similar to the prepotentials noted by Sozler (17) in the ureter. The local potentials were found over all of the uterus rather than in one isolated area, as in the ureter.

By placing two electrodes on the uterus parallel to the long axis of the horn, synchronous activity at two different places on the uterus was observed. One area usually lagged slightly behind the other. In the rat, the longest distance over which there was synchronous activity was 5.4 cm. Over longer distances the activity was partly synchronous and partly independent.

The synchronous activity was related only to the series, not to the individual potentials. However, if the electrodes were placed a few mm. apart there was synchronization of the spikes. The greatest interval at which this occurred was 13 mm. in the cat and 13 mm. in the rat.
coordination of both the series and the spikes was much better when the electrodes were placed in the longitudinal direction than when they were placed transversely.

The form of the potentials changed frequently from wave to wave. This may have been due to either the interference of alternating pacemakers, or propagation of the excitation wave traveling at varying distances from the electrodes. He concluded this was due to the latter and theorized therefore, that excitation in smooth muscle may be conducted over different pathways.

There were variations in the distances separating electrodes which would show synchronization of the spikes. He theorized that this demonstrated how much the ability to conduct is subject to variations, and how two areas can function with a different autonomous rhythm. He believed this could be explained by a total blocking of excitation similar to blocking of conduction in the heart by an area which is already excited.

In the cat, excitation arrived at the caudal electrode first 60 per cent of the time, and at the cranial electrode first 20 per cent of the time. The remaining 18 per cent was simultaneous.

Stimulation of the cervix results in the appearance, within a fraction of a second, of a series of spikes under electrodes placed on opposite horns. From this he concludes
a series of spikes which produced a true tetanus. The individual spikes had a duration of 0.2 to 0.3 seconds, but if a smaller wire was used, the duration was recorded as approximately 30 ms (milliseconds). The frequency of the spikes varied slightly, being greater in the cat. Local potentials, or shallow oscillatory vibrations of potential occurred slightly before the first spike in a series. He concluded that these were similar to the prepotentials noted by Bozler (17) in the ureter. The local potentials were found over all of the uterus rather than in one isolated area, as in the ureter.

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In the cat, excitation arrived at the caudal electrode first 63 per cent of the time, and at the cranial electrode first 20 per cent of the time. The remaining 17 per cent was simultaneous.

Stimulation of the cervix resulted in the appearance, within a fraction of a second, of a series of spikes under electrodes placed on opposite horns. From this he concluded
that cervical stimulation resulted in neurogenic transmission of excitation, possibly through a reflex arc involving certain spinal cord segments.

From his experimental observations he noted that all areas of the uterus were capable of autonomous excitation, but it appeared that the ovarian end was driven to a certain extent by the cervical end since the cervical end was the most active.

In summary, he stated that the above evidence confirms Bozler's assumption of the syncytial nature of the myometrium, and that every part of the myometrium has the capacity to become a pacemaker; however, the cervical end has a greater excitability than the ovarian end.

West and Landa (104) investigated the electrical activity of the pregnant rat uterus just before parturition, using intracellular microelectrodes.

The resting potential averaged 42.3 mv. and the average action potential was 27.7 mv. The action potentials appeared in trains of 30 seconds duration, followed by a quiescent period of 1.5 to 2.0 minutes. The frequency of the action potentials in the trains increased from three in the first 5-second period, to approximately five in the center of the burst, and then decreased to less than one
at the end of the series. During the peak frequency, and during the declining phase, there were prepotentials in the intervals separating spikes.

When contractions were recorded simultaneously with the electrical activity, the action potentials began to appear with the onset of contractions and during relaxation no action potentials were apparent.

The relationship of contractions to action potential frequency suggested that interfiber spread of excitation could be a function of mechanical deformation of the cells.

Thiersch, Landa, and West (101) investigated the electrical activity of the uterus of the rat in different stages of pregnancy, postpartum, and nongravid. Intracellular microelectrodes were used. The placental areas were compared to the nonplacental areas. With advancing pregnancy there was an increase in the resting potential in the interplacental areas. At 12 days of gestation there was a marked difference between the two areas.

In general the spike frequency and duration of the trains were least in the placental areas. There were frequencies of 3.5 per 5 seconds increasing to 4.5 per 5 seconds in the nongravid uterus; 3.0 increasing to 3.5 at 12 days; 4.2 increasing to 4.3 at 15 days; and 3.0
increasing to 3.5 per 5 seconds at 21 days. In the postpartum uterus the frequency was 1.3 per 5 seconds and remained steady for 35 seconds.

Prepotentials appeared in a small percentage of series at 15 days while at 21 days 31 per cent of all series had prepotentials. Twenty-four hours postpartum it had decreased to 53 per cent. They were not seen at all in the nongravid uteri or in the 12-day pregnant uteri.

The train duration at 15 days of pregnancy was shortest and increased in order from the 12-day uteri, to the nonpregnant, to 21-day pregnant, and the greatest in the postpartum uteri.

There was no correlation of the resting potential with the frequency of the action potentials, except when the 21-day pregnant uterus was compared to the nongravid uterus. The presence of the prepotentials at 21 days indicated increasing numbers of the myometrial cells are capable of self-excitation as pregnancy progresses. The functional culmination of these changes could be mass excitation and contraction associated with the termination of pregnancy.

In a coincident report Landa, West, and Thiersch (72) used surface electrodes and recorded the electrical and mechanical activity from 21-day pregnant rat uteri.
When using large strips it was apparent that the electrical activity was associated with the mechanical, but there was no definite relationship. The maximum spike frequency and peak contraction, onset of spikes and onset of contraction did not always coincide and tension could be recorded in the absence of any electrical activity. In smaller segments the action potentials preceded the onset of contractions and the total contraction terminated just after the final spike in a train. Peak spike frequency was associated with peak contraction. Their records showed the tetanic nature of the contractions as was pointed out previously by Bozler (16) and Jung (55).

When electrodes were placed transversely on the strip, 2 cm. apart, dissociation of activity was complete. At 7 mm. and at 1 mm. there was coordination. In the smaller segments coordination was present even at the extreme ends of the strip. When coordinated, the interpotential time varied widely, even though the spike frequencies were identical.

They concluded there was no evidence for the syncytial propagation of impulses, except in very small segments. The coordinated, summated contractions of the small segments and their relationship with the spikes suggested the presence of a controlling mechanism for impulse propagation.
from a single depolarization. The spike amplitude and rate
of depolarization were roughly proportional to the initial
membrane potential.

With surface electrodes the action potentials averaged
1 to 3 mV. amplitude and 15 to 30 msec. duration. They
moved at a rate of 9 to 12 cm. per second along the
longitudinal axis, in either direction, for distances up
to 2.0 cm.

Jung (54, 53, 59) used fibers from pregnant rat uteri.
Microelectrodes were inserted to record the electrical
activity. Uteri 24 hours prior to delivery, or in delivery,
had more variable resting potentials and more spontaneous
activity than did a group one to four days prior to
parturition. The resting potential averaged 41 mV. and the
action potentials were from 2 to 70 mV. There was a linear
relationship between the magnitude of the resting potential
and the magnitude of the action potential. The greater the
resting potential the greater the action potential. There
was an occasional overshoot but it occurred irregularly.
It would sometimes rhythmically appear and disappear. One
to four days prepartum the overshoot was rare, but during
parturition it was relatively common. Fibers showing
rhythmic formation of prepotentials were considered as
pacemaker fibers.
They proposed four theories of myometrial conduction: (1) electrical conduction without decrement following a definite pathway; (2) electrical conduction without decrement following an indefinite pathway; (3) electrical conduction with decrement following an indefinite pathway; (4) propagation mediated by mechanical deformation. The latter could limit electrical activity to single fibers with interfiber spread mediated by mechanical activity and deformation of adjacent cells. They believed the last to be correct and in support of this they noted that pre-contractions preceded the onset of fast contractions and electrical activity. This caused stretch which decreased the membrane potential to threshold. The first spike in a train often repolarized to a value greater than before and thereafter a prepotential often preceded each subsequent spike.

Daniel and Singh (23, 31) used intracellular and extracellular electrodes to describe the electrical activity of the pregnant cat uterus. With microelectrodes the resting potential was 40 to 60 mv. The action potentials averaged 20 to 40 mv. with overshoots of 2 to 11 mv., usually less than 10 mv. The duration of the spikes was 250 msec. or much longer when multiple spikes originated
Goto and Woodbury (43) recorded the electrical activity of the pregnant rat uterus and its relationship to tension. Using microelectrodes there was a resting potential of 33 mv. during quiescent periods. The action potentials varied in height and duration and occurred four to nine times per second in 30-second long trains. The average amplitude was 27 mv. and duration 70 msec. In most of the cells, the resting potential changed about 3 mv. between the action potentials. This resembled pacemaker potentials. They concluded that some cells act as pacemakers, thereby increasing the excitability of adjacent quiescent fibers. Tension started to increase a few seconds after the first action potential in a train. The time course of tension change was similar to but lagged behind the firing frequency curve. Increasing the tension by passive stretch or contraction reduced the membrane potential.

Goto and Csapo (41) using the same technique, reported the effect of the placenta on the electrical activity of the rabbit uterus. From 20 to 30, or 31 days, of gestation the membrane potentials at placental implantation sites were higher than the interplacental sites. The onset of labor was preceded by a drop in the membrane potential at the placental sites producing a more or less uniform membrane
potential of 45 to 50 mv. all along the uterus. After parturition the membrane potential dropped to 30 to 35 mv.

Continuing along similar lines Kuriyama and Csapo (69) used the same technique on pregnant rabbits. During the last third of pregnancy the membrane potential increased to 60 mv. at the placental sites and there were no regular trains of action potentials. Delivery occurred at a membrane potential of 50 mv. They concluded that regular phasic mechanical activity was closely linked to regular trains of action potentials of appropriate amplitude and frequency.

Kuriyama and Csapo (71) recorded the electrical activity of the parturient and postpartum rat and rabbit uterus. They used intracellular microelectrodes and simultaneously recorded the mechanical activity.

The postpartum uterus had a stable membrane potential of 50 mv. at rest. The action potentials appeared in 25-second trains of 30 action potentials each. The trains appeared at about 50-second intervals. The amplitude of the action potentials was about 50 mv.

They noted three types of train discharges: (1) a train preceded by a slow depolarization wave; (2) each action potential in a train preceded by a prepotential; (3) train discharges without preceding slow waves or
prepotentials. The slow depolarization sometimes continued after the first action potential was discharged. This coincided with an increase in spike frequency and a decrease in amplitude. During the second half of the train the membrane potential increased, spike frequency decreased, and amplitude increased again, showing there was an inverse relationship between spike frequency and amplitude.

Their observations suggested that any or all of the myometrium can become a pacemaker. The prepotentials may or may not give rise to propagated action potentials since its effect depends upon the relationship of its arrival time to the excitability cycle of the cell. Occasionally there were irregular trains of discharges which may have been due to potentials generated in adjacent cells, or a change in the duration of the refractory period.

They compared the parturient or postpartum uterus with the uterus earlier in pregnancy. The membrane potential was high and excitability and conduction were depressed late in pregnancy. The action potentials were irregular and not in synchrony with the mechanical response. It was the parturient or postpartum uterus which displayed regular electrical activity well synchronized with the mechanical response.

Joto et al. (42) recorded from the pregnant mouse myometrium using microelectrodes. They electrically
stimulated uterine strips to determine the refractory period and rate of conduction. The absolute refractory period was 0.1 sec. and the relative refractory period was 0.2 sec. Conduction of excitation was 10.2 cm. per second in the same muscle bundle and slower and variable between different muscle bundles.

Kuriyama and Csapo (70) reported on conduction of excitation in the rabbit myometrium. There were four points marked on loaded uterine strips with fluorescent dye. The movements of these points were recorded with a motion picture camera.

In early pregnancy there was no propagation. In late pregnancy in the non-gravid horn, there was some propagation but only moderate activity. In the pregnant horn there was propagation between sites of placental attachment but none across the placental areas. Propagation in the parturient or postpartum uterus varied with the degree of placental detachment. There was a response between the two stimulating electrodes in all of the preparations. They concluded that the uterus was always capable of responding but not of conducting excitation.

Soto and Csapo (40) recorded the membrane potential of the pregnant rabbit myometrium with intracellular micro-electrodes. From the twentieth to the twenty-ninth day
there was a membrane potential of 60 mv. in the placental sites and 43 mv. in the interplacental areas. Near parturition the membrane potential dropped in the placental areas and at parturition there was a uniform membrane potential of 50 mv. in the placental and interplacental areas. A few days postpartum the membrane potential was 35 mv. They concluded that the membrane potential was subject to endocrine regulation, and that the membrane potential changes could be correlated with myometrial function. There were local potentials of varying frequency in the same cell. This was explained on the basis of intercellular bridges conducting electrical activity from one cell to another.

Along similar lines, Kumar and Barnes (67) reported similar results from the human uterus. They used external electrodes placed on strips of myometrium obtained at Cesarean section. The resting potential at 33 weeks was higher in the placental than in the nonplacental sites. In two cases, after 33 weeks of gestation, there was very little difference between the two sites.

Kao (613) used conscious unrestrained rabbits, which had electrodes implanted on the uterus for periods up to 3 weeks. There were slow oscillations of potential which increased in frequency and amplitude during the latter half
of pregnancy. Shortly preceding and throughout parturition spikes began to appear in frequent and sustained bursts. The spikes reached 2 to 3 mv. and occurred approximately 0.5 second apart. Postpartum there were only small oscillations of potential.

Kao (62) continued the above experiments. He used mature rabbits and implanted 0.5 mm. loops of silver wire. The wire was coated with silver chloride. They were placed on the free border of the uterus between adjacent fetuses. The indifferent electrode was located in the parametrium or myometrium between the two recording electrodes.

The slow waves were similar to those discussed in the 1953 report. The action potentials lasted 200 to 300 msec. and had an amplitude of 0.3 to 3.0 mv. The frequency and amplitude increased towards parturition and declined in the postpartum period. Action potentials often followed one another at intervals of 750 msec. This fact was given as evidence that the refractory period is somewhat less than 750 msec.

The cervical and ovarian ends were equally active, but rarely did one mirror the activity present at the other.

Bursts in the two horns often coincided with one another, which led him to believe there may be some central controlling mechanism.
During the twentieth to thirtieth day of gestation, there were only slow oscillations of potential; at 30 days the oscillatory variations dominated the recordings and even increased some in amplitude. The frequency of action potentials ranged from 3.7 to 55 action potentials per minute. The action potentials increased in amplitude and number each day, but at 5 hours prepartum there was a sharp increase in the number of action potentials due to the increase in frequency of the action potentials and duration of the bursts. The activity waned slowly after parturition.

When comparing the activity of a nonpregnant and a pregnant horn in the same animal the trend was the same in both, but the pregnant horn was several times more active and the activity in the nonpregnant horn was more variable. This suggested that the activity of the nonpregnant horn was not as well synchronized.

He theorized that coordinated activity in the myometrium is possible through some neural or humoral mechanism, which initiates the impulses. These are then modified according to the prevailing local conditions such as tension, size of the uterus, and size of the cells.

Daniel and Renner (30) reported on the effect of the placenta on the electrical activity of the cat uterus in vivo and in vitro. One mm. diameter discs of silver
were attached to polyethylene insulated wires. The discs were placed just under the serosa, which was then sutured over the discs. The wires passed under the skin to a point between the shoulder blades where they emerged. An indifferent electrode was inserted into the abdominal wall. The electrodes were placed one on either side of the placenta, one over the placenta on each horn, and one on the body of the uterus.

The electrical activity appearing at all electrodes for a period of one week following insertion was different from that which occurred later. Therefore, recordings obtained during the first week were not considered reliable.

They also used some uterine strips. One half of the strip was from the placental area and one half from the nonplacental area.

The action potentials differed somewhat in vitro and in vivo. In vitro they were 1.0 mv. in amplitude, 25 msec. in duration, conducted at 3.0 to 12.0 cm. per second and appeared at intervals as short as 150 to 200 msec. In vivo the amplitude was the same but the duration varied from 40 to 250 msec., were conducted at 9.0 to 10.0 cm. per second, and appeared at intervals of not less than 300 msec.

There was very little spontaneous activity prior to term, although there were some tetanic bursts of action
potentials at the interplacental sites. At the placental areas the activity varied from none, or a few action potentials, to bursts similar to those in the nonplacental areas. The bursts tended to be short, 30 seconds, as compared to parturition when they were 25 to 100 seconds, the average was 60 seconds. At term the activity usually started at the electrode nearest the fallopian tube. There was no consistent pattern of spread. The electrical activity consisted of long sustained bursts of action potentials resulting in prolonged force by the myometrium. They concluded that the peristaltic propulsive activity at term is due to the nonexcitable band of placental myometrium.

Daniel (29) studied the activation of the myometrium during stretch-induced contractions. Uterine strips from rats, cats, rabbits, and humans under 5.0 grams resting tension were used. The mechanical activity was recorded simultaneously with the electrical activity. The electrical activity was recorded with differential pore electrodes placed on the long axis of the strip 0.3 to 1.5 cm. apart.

The 5.0 grams of tension initiated activity in all strips from pregnant animals. The action potentials were triphasic with first a positive deflection, then a negative
deflection, and then another positive deflection, usually one fifth to two fifths of the amplitude of the negative deflection. There were several variations in the above, such as: (1) an increase in positive deflection without the negative phase, which probably indicated the action potentials approached but did not pass beyond the electrodes; (2) the action potentials acquired a negative phase, indicating they appeared to spread beyond the electrode; (3) the action potentials became prolonged, indicating that conduction was slow, or; (4) negative deflections appeared independently at each electrode, indicating failure of conduction.

The amplitude of the action potentials varied from 0.66 to 1.65 mv. They were conducted at 3.0 to 12.5 cm. per second in the pregnant cat uterus. The interval between action potentials was 155 to 217 msec., a crude approximation of the refractory period. The action potentials occurred in bursts of 10 or more potentials. The bursts usually ended by a successive slowing of the action potential frequency.

The action potentials were noted in most or all areas of the strip before maximum tension was reached and had ceased in most areas before relaxation began. In some preparations there were action potentials before any increase in tension was recorded.
There was no relationship between action potential frequency and tension. An increase in the length of the bursts caused an increase in the duration of the contraction. Propagation was from cervical to tubal, tubal to cervical, or started in the middle and spread both ways. There was conduction failure and increased threshold to stretch in some of the strips which had overlaid the placenta.

They concluded that, from the nature of the electrical activity, large numbers of cells were active simultaneously, indicating that spread of a wave of depolarization is by means of local currents in a volume conductor, at least over limited distances. There was no evidence of the existence of a syncytium and no nerve fibers have been reported to exist in uterine muscle arranged in a manner to propagate conduction.

Kuriyama (63) reported some of his work and reviewed that of others on the electrophysiology of the uterus. The membrane potential increased during pregnancy but was considerably lower at parturition. It was higher in the placental areas than in the nonplacental areas.

In general, the size of the action potentials corresponded to that of the membrane potential. An overshoot was recorded in most of the species studied. The size of
the action potential differed between the pregnant and postpartum uterus and between the placental and nonplacental areas. The frequency and number of spikes in a burst varied between the pregnant and postpartum uterus. The pregnant myometrium averaged two action potentials per second and 23 per burst. The postpartum myometrium averaged 1.3 per second and 21 per burst. Usually the action potentials followed the all or none law, but this was not true for the pregnant myometrium.

Pacemaker or prepotentials were found in all parts of the uterus and were not specific to one area. They often changed from one area to another.

Local or electrotonic potentials were often seen in propagating cells at the end, or beginning, of a train discharge. They were often seen at parturition or postpartum.

Conduction may be syncytial or electrotonic. Conduction velocity varied from 1.0 to 9.5 cm. per second. Tubal to cervical conduction was 13.3 cm. per second, and cervical to tubal was 7.0 cm. per second. There was a difference between placental and nonplacental areas.

The number of spikes and the duration of the train was directly related to the amount and duration of tension. Incomplete tetanus could be changed to complete tetanus by an increase in the frequency of the action potentials. In
early pregnancy the spikes were small and the contractions appeared as small tonic contractions. During late gestation there were irregular spikes which were not clearly related to tension developed by the whole tissue, but it was noted that contraction was a function of the whole tissue and electrical activity was a function of only a few cells. The postpartum myometrium showed a clear relationship between the spikes and the development of tension.

With a conduction rate of 15 cm. per second and a rate of 1 second for contraction to reach maximum there is enough time to enable the whole organ to contract and expel the fetus.

Jung (4) in reviewing his own work in 1962 discussed conduction and the existence of pacemakers in the myometrium. The frequency of the action potentials could be up to eight per second, and synchronization of these usually was found at sites up to a few cm. away from each other, but two distinct rhythms could be recorded from two different points on the surface of the uterus.

Propagation of the impulses was related to the longitudinal muscle fibers on the surface of the uterus but successive individual impulses did not always follow the same pathway. Disturbances of conduction ranged from delayed conduction to complete block.
The impulses originated from a large number of independent pacemakers. Individual pacemakers were responsible for areas of stimulus formation whose size varied and in which their rhythm either blocked that of neighboring areas or took up the rhythm from neighboring areas. The size and location of these pacemaker areas varied greatly.

In a recent review on smooth muscle physiology Csapo (17) reported that all cells of the myometrium almost never worked in complete synchrony and that uterine function was graded by the ratio of active to inactive cells. Early in pregnancy there was asynchrony and irregularity between the electrical activity and the intra-amnionic pressure, while at parturition there was almost complete synchrony. Therefore, the characteristic properties of parturition were regularity of uterine function and synchrony between mechanical and electrical activity.

Bozler (20) stated that all fibers of the myometrium could show prepotentials and initiate function and they could alternate in this function. It appeared to him that the prepotentials and the associated increase in tension originated within the cell, and that variations in metabolism are the basis for automaticity.
no definite pathway of conduction, and no definite point of origin. There was no similarity from patient to patient and there was no evidence of a pacemaker.

Steer and Hertsch (100) reported complex waves of 100 to 500 microvolts at a frequency of 0.5 to 2.0 cycles per second. The potential changes were noted first over one cornu and as labor progressed were seen next over the opposite cornu and eventually over the fundus. There was practically no activity in the lower uterus. They theorized that there was a pacemaker in early labor and that in strong labor, when all three points were active simultaneously, the activity could begin at several points or there could be very rapid spread from the pacemaker.

Steer (93) made a more detailed report of the fast electrical activity. He reported that there were biphasic electrical waves of 50 to 500 microvolts occurring at frequency of one to two cycles per second. These potential changes occurred intermittently, began with the onset of a contraction and ended as relaxation began. The total duration of the electrical activity varied with the clinical duration of the contraction. He concluded that the frequency of the potential changes was no more important than the amplitude. In general, the "stronger" the electrical activity the more rapid was dilation of the cervix.
Prosseer (33) discussed the conduction in smooth muscle and reported that there were four theories: (1) conduction within nerves running parallel to the muscle fibers; (2) conduction by a mechanical pull from fiber to fiber; (3) conduction by a chemical transmitter; (4) electrical conduction through a sheet of smooth muscle, as in a functional syncytium with the properties of a core conductor.

He discussed the arguments pro and con and concluded that smooth muscle is a functional syncytium with intercellular summation.

**External Hystero graphy in Women**

...node, cited by Reynolds (30), employed needle electrodes at the level of the umbilicus in pregnant women and reported a deflection of the galvanometer during a contraction of the uterus. Clason (24) employed plate electrodes on women in labor and found that slow diphasic electrical currents appeared synchronously with the contraction.

Dill and Halden (33, 34) were the first to make extensive use of the external hystero graph. They reported slow changes in potential which had no reduplicable pattern,
In a later report in 1959 Steer (99) described slow waves of potential in addition to the rapid changes already described. The waves had a duration of 1 to 2 minutes. He theorized that the slow waves were large alterations of standing surface potential and the fast deflections were basic electrical activity from which the surface potential was derived.

Halliday and Heyns (45, 46) reported on the use of surface electrodes. They used one electrode on the abdomen and an indifferent electrode on the arm.

The data was variable. It was impossible to recognize changes in amplitudes or duration of the potential changes in normal and abnormal labor. However, the amplitudes from the upper and lower segments of the uterus could be compared. In early labor the amplitude of the potentials from the upper and lower segments were usually equal. As labor progressed the amplitude of the potentials from the lower segment became increasingly less than those from the upper segment.

They discussed the change in pressure in the uterus and believed that the theory of fundal dominance for efficient dilation of the cervix was inaccurate since pressure was transmitted equally to all parts of the uterus.
Therefore, the cervix would continue to dilate regardless of whether the fundus was the most active or not.

Larks (73, 74, 75, 76, 77, 73) and his co-workers have made detailed studies of the electrohysterograph. They recorded biphasic waves of approximately 6 minutes duration. The electrical activity increased from the thirty-fifth week onward. Prior to parturition the great variability and lack of pattern suggested multiple foci and localized events or sporadic pacemaker activity. The appearance of major slow diphasic waves indicated conduction and spread of waves of excitation. It appeared, therefore, that toward the end of gestation pacemaker activity, conduction of waves of excitation and muscular responses were initiated in that order.

Corey (25) compared external electrohysterography to recordings obtained from uterine strips, from whole organs suspended in oxygenated Locke's solution, or directly from the uterus at Cesarean section. There were complex diphasic waves of 11.6 seconds duration. He concluded that these were due to uterine activity and not to that of neighboring tissues or viscera.

Hon and Davis (51) performed a similar study. They compared the skin potentials with the recordings made directly from the uterus during Cesarean section. There
required to deliver the fetus. Duncan cited by Reynolds (90) and Dodek (35), elaborated on Poppel's work and calculated the average force on the fetus as 16.73 pounds.

Joulin, cited by Harris and Gillespie (47), used a pair of delivery forceps fitted with a spring and scale. By preventing delivery of the fetus with the forceps he arrived at 110 pounds as the force applied to the fetus.

Schatz in 1372, cited by Dodek (35), Harris and Gillespie (47), and Reynolds (90), is generally credited with being the first to use a balloon in the uterus to record the intrauterine pressure. Poullet, cited by Reynolds (90) and Dodek (35), expanded the technique slightly by placing a second balloon in the rectum. The results were not very reliable due to contractions of the rectum and pressure of the nearby uterus.

Heinricium, cited by Falk and Nahon (36), using the same technique noted three deflections of the manometer: (1) pulse, (2) respiration, and (3) uterine contractions which lasted from 30 seconds to 3 minutes.

Westermark, cited by Reynolds (90), Dodek (35), and Harris and Gillespie (47) was the first to object to the large size of the balloon. He noted that its use was dangerous, required anesthesia, and resulted in increased uterine contractions due to its bulk. He used a 2.0 ml.
was a marked dissimilarity between the two areas. They also demonstrated skin potentials, similar to those seen in labor, in a male patient when the skin was stretched. They concluded that skin potentials may not accurately reflect uterine potential changes.

Bergstrom and Bergstrom (3) studied the effects of respiration on the electronystagrogram. They concluded that the potential variations seen in labor were partly attributable to the uterus, but could be modified by respirations.

Kormesser and Nyboer (56) reported recordings of external potentials very similar to those of Larks and Dasgupta (77).

**Intrauterine Pressure**

The earliest objective observations on uterine forces were those of Poppell in 1863, cited by Reynolds (90). He noted that the fetus was often delivered shortly after rupture of the membranes and therefore concluded that the force required to rupture the membranes could not be far from that required to deliver the fetus. The amount of force required to rupture the membranes in vitro was measured and considered as an approximation of the force
balloon attached to an elastic membrane manometer for a low inertia system. The strength of the contractions increased as labor progressed, reaching a maximum as the fetus was expelled.

Rucker (95) used the intrauterine bag to study the effects of drugs on the uterus. His records indicated there was a rhythmic occurrence of the contraction waves in the uterus. The frequency varied from one per minute to one per 10 minutes.

Bourne and Burn (11) used a flat rubber balloon with a wire loop inside. The balloon was inserted between the placenta and the wall of the uterus. The intrauterine pressure during the first stage of labor was 63 mm. of Hg and during the second stage was 200 mm. of Hg.

Moir (35, 36) recorded intrauterine pressure from the fundal and cervical portions of the uterus at the same time. Most of the time the two portions were independent of each other. The pressure in the cervical portion began to rise when the pressure in the fundal portion was or had just passed the peak of its contraction. The recordings were taken during parturition and postpartum.

Moir reported a resting intrauterine pressure of 15 mm. Hg. The average for the first stage of labor was 60 mm. Hg which included the resting pressure. The average for the
second stage was 105 mm. Hg, which included the resting pressure and bearing down. He compared the intrauterine pressure with the pressure in the umbilical vein to determine if the bag caused any artifacts. The pressures were similar and he concluded that the bag does not alter the normal contractions of the uterus.

Adair and Davis (1) used the intrauterine balloon technique to study the effects of drugs on the uterus immediately after delivery of the fetus. There were normal contractions occurring every 4.3 minutes and lasting 2 minutes. The intervals between contractions were regular, but the strength varied from contraction to contraction.

Woodbury et al. (111) compared the abdominal, uterine, and arterial pressures during labor. They used balloons in the stomach, and the uterus, and recorded brachial artery pressures. Intrauterine pressure and gastric pressures were compared with a differential manometer. Similarly, they compared the brachial artery pressure with the maternal placental pressure.

Uterine contractions resulted in smooth symmetrical pressure rises of 25 to 95 mm. Hg. During delivery of the head the maximum expulsive force was 15 kilograms. During the early stages of labor the intrauterine pressure was the
Venable (102) studied the problem of retained fetal membranes in the cow. A 4-inch rubber balloon was placed deep into the uterus and connected to a mercury manometer. The balloon was filled with air.

At 2 hours postpartum rhythmic contractions occurred at an average rate of 14 per hour. The amplitude was 40 to 50 mm. of Hg. The rate and amplitude decreased as the time after parturition increased.

Wieloch (106) in 1927 was the first to use trans-abdominal puncture of the uterus and amnion. A catheter was placed inside the amnion of pregnant women via a midline incision. The catheter was connected to a water manometer. There were 5.0 to 15 cm. water pressure. He concluded that the intrauterine pressure is minimal and the uterus adapts to any volume.

Mayer, cited by Reynolds (90), made a similar study.

Alvarez and Caldeyro (2) were the first to make extensive use of the intra-amnionic catheter in humans. A catheter was inserted into the amnion by a transabdominal puncture. At the same time, urinary bladder pressures were recorded. In the third stage of labor the placental blood pressure was recorded.

From the ninth week to the end of pregnancy there were 10 to 30 rhythmic contractions per 10 minutes. They had
same throughout the uterus. Straining in early labor had no expulsive effects since its force was directed all around the uterus.

Salerno (96) recorded the "relative" intrauterine pressure, or the difference between the standing pressure and that caused by contractions of the uterus. A bag 11 cm. in diameter was inserted into the cervix and removed when the cervix was completely dilated. The average "relative" pressure was 32.1 mm. Hg and it never exceeded 125 mm. Hg. This included "bearing down" by the woman.

Jordan (53) studied the uterine motility of the cow in the puerperium. A balloon was placed in the posterior part of the recently gravid horn and distended to 4 inches by 2 inches. It was connected to a mercury manometer.

From 0 to 12 hours postpartum there were 13.3 contractions per hour with an average amplitude of 20.2 mm. Hg. The onset of the contractions was relatively sudden. The pressure rose to a peak in an average time of 0.7 minutes and stayed at this level for 1.0 to 1.5 minutes, then returned to the baseline in approximately 1.0 minute. As the time after parturition increased, the frequency and amplitude of the contractions decreased.
an intensity of 0.3 to 7.0 cm. of water. There were sporadic Braxton-Hicks contractions of over 3.0 cm. of water. During the last two weeks the intensity and frequency of the Braxton-Hicks contractions increased and the rhythm became more regular. The frequency was three to nine contractions per 10 minutes.

During the first and second stages of labor there were two to six regular, strong contractions per 10 minutes. The frequency varied inversely with the square root of the intensity.

Alvarez and Caldeyro-Barcia (3) connected the umbilical vein to a mercury manometer to record the pressure exerted on the placenta by the contractions of the upper segment of the uterus. The contractions were continuous with those of the second stage of labor. The intensity was 50 mm. Hg and the frequency averaged 4 per 10 minutes.

Alvarez and Caldeyro-Barcia (4) recorded the intramuscular pressure of the myometrium with small, 0.1 ml. capacity, balloons simultaneously with intra-amnionic pressure. Prior to labor there were small, 1.0 to 5.0 mm. Hg rhythmical oscillations of amnionic pressure occurring every 3 minutes. The recordings from the intra-myometrial balloons indicated that these were due to
localized contractions of the myometrium. They originated in different parts of the uterus and spread very slightly from their point of origin.

The Braxton-Hicks contractions lasted from 30 seconds to 3 minutes or more and produced increases of 10 to 20 mm. of Hg in intra-amnionic pressure.

The change from the contractility of pregnancy to that of labor was characterized by an increase in the frequency and strength, more regular rhythm, and a decrease in the duration of the Braxton-Hicks contractions. The small oscillations gradually decreased until they disappeared in labor. Although these contractions, as recorded with the intramyometrial balloons were equal in intensity prior to labor and in labor, they did not dilate the cervix since they lacked coordination and spread of the contraction.

In labor the contractions started near the uterine end of one of the fallopian tubes and spread mainly downward over the entire uterus within a few seconds. Usually there were two pacemakers alternating from one side to the other. In some patients one side predominated. The contraction wave lasted longer at the pacemakers than at other sites. The waves reached their peaks and ended simultaneously at
effect of drugs on labor in women. From the records, the intra-amnionic pressure was 20 to 60 mm. Hg during contractions and occurred at a frequency of 5 to 3 per minute.

Ramsey et al. (39) used anesthetized monkeys and recorded from the intervillous spaces and the amnionic cavity. The catheters were connected to strain gauge pressure transducers. In mid-pregnancy the amplitude of the contractions was less than 20 mm. of Hg; at the end of pregnancy the amplitude was greater than 20 mm. Hg in five of nine monkeys.

The average tonus was 1.0 to 6.0 mm. Hg. During mid-pregnancy the contraction cycles were longest, in one third of the animals the periods of tonus predominated. Shorter cycles with brief periods of tonus characterized prelabor.

Bieniarz and Reynolds (9) compared the intrauterine pressure of pregnant sheep to fetal and maternal circulation and blood pressure. A polyethylene tube was inserted into the amnionic cavity through an incision in the uterus and held in place with a purse string suture.

The intrauterine pressure was not discussed as such, but from some of the tables and records the basal intrauterine pressure appeared to be 4.0 to 5.0 mm. Hg.

Lindgren (79) made a detailed study of amplitude and frequency of contractions during labor by means of a catheter inserted into the amnionic cavity of women.
all sites. After labor the spread of the waves became much slower and hence was a "peristaltic-like" wave, one part of the uterus contracted and another part relaxed.

Caldeyro-Barcia and Poseiro (22) used the same techniques to study the effects of oxytocin on the human uterus. The preinjection normal recordings agreed very closely to the above.

Williams (107) and Williams and Stallworthy (103) used a polyethylene catheter inserted through the cervix into the amnionic cavity. The tube was perforated at several places on the end to avoid obstruction by the membranes or fetus. The tube was connected to a mercury manometer placed at the level of the pubis of the patient.

The "basal" intrauterine pressure was 3.0 mm. Hg. The first stage contractions produced a pressure of 40 to 90 mm. Hg and the second stage, with bearing down, a pressure of 130 mm. Hg maximum. Systole was more abrupt than diastole. They considered 30 mm. Hg in the first stage as the maximum safe pressure and less than 20 mm. Hg as the normal basal intrauterine pressure.

Carey (23) used a polyethylene catheter with an S-shaped stylette. The catheter was inserted into the amnion and the stylette withdrawn. The paper dealt primarily with the
Primigravidas required the most uterine work, plurigravidas in the 20- to 29-year old group required the least. Uterine work was independent of the weight of the fetus, and the total work at term was not affected by the length of labor.

Labor consisted of four or five rhythmic contractions per 10 minutes, each one lasting 40 to 50 seconds. The average intensity was 40 to 60 mm. Hg.

Hendricks et al. (50) used four catheters inserted into the uterine wall. They first had satisfied themselves that the pressure within the uterus is homogeneous and that the pressure within the uterine wall was an accurate reflection of the intrauterine pressure.

The average pressure due to contraction of the uterus was 70 to 90 mm. Hg, and the frequency of contraction was two to three per 10 minutes.

In early labor uterine activity was 150 MU (Montevideo Units). These were defined as the average frequency of contractions, times the average pressure. The activity reached a peak of 300 MU in late labor. Postpartum in one patient, the activity was 335 MU shortly after delivery and decreased to 200 MU in one and one half hours, where it stabilized. In another patient the activity was 300 MU in early postpartum and decreased to 300 MU at one and
During the first stage of labor the frequency of the contractions was one per 3 minutes. In the second stage it was two per 3 minutes. In primipara the frequency ranged from 13.6 to 23.5 contractions per hour, but in multiparas it ranged from 23 to 25.3 per hour.

If the initial amnionemic pressure was taken as zero the pressure during the first part of the first stage of labor averaged 6.2 mm. Hg, 7.0 during the second part of the first stage, 22.0 during the first part of the second stage and 32.7 during the second part of the second stage of labor. Bearing down by the patient produced pressures of 104.7 to 121 mm. Hg.

The frequency was related to pressure, tone, rate of cervical dilation, and duration of the second stage of labor. As pressure increased the frequency decreased. The relationship of tone and frequency were fairly constant, but there were slight increases in tone with increased frequency. As the frequency increased the rate of cervical dilation increased, a decrease in frequency resulted in an increased duration of the second stage of labor.

Burnhill et al. (21), recorded the amnionemic pressure during labor. The uterine work was estimated, and compared in various groups of women.
one half hour. They believed the greater postpartum activity was due to the relatively larger bulk of the uterus contracted around the much smaller contents of the uterus. The uterus gradually developed a pattern of contractility marked by irregularities of the contraction cycle. This was characteristic of the incoordination present before active labor began.

In contrast Méndez-Sauer et al. (34) recorded the intramuscular pressure of the human myometrium with latex balloons. The balloons had a capacity of 20 cm. A column of mercury was used between the balloon and the transducer to absorb the high basal pressure necessary to distend the balloon.

The intramuscular pressure was influenced by changes in the area of the balloon and not by changes in distant areas.

Several balloons were placed in different parts of the uterus of a woman during a Cesarean section. All contractions were seen first from the balloon nearest the fallopian tube. The contractile wave spread slowly and the duration of the contraction became shorter as the wave moved away from the fallopian tube. The intramuscular pressure was the highest in the upper segment of the uterus.

Pilette and Holm (33) recorded the intrauterine pressure with small balloons placed between the myometrium
and the mucosa of the pregnant cow's uterus. These pressures were compared with those from a balloon placed in the abdominal cavity.

There was a change from small, short duration contractions to large, long duration contractions as parturition approached. The intrauterine pressure at parturition averaged 130 cm. of water. They concluded that the uterus contributed 90 per cent or more to the expulsion of the fetus.

Corner et al. (26) recorded from the amnionic cavity or the intervillous spaces of the placenta of monkeys.

In early pregnancy there were high amplitude short contraction cycles. The duration of the contraction phase exceeded that of the relaxation phase. In mid-pregnancy there was relative quiescence. Low amplitude contractions occurred at longer intervals. The relaxation phase was sometimes longer than the contraction phase. In late pregnancy there was increasing amplitude and frequency of contractions.

During labor the contraction waves were high amplitude and occurred in rapid sequence. The amplitude was in the same general range as in early pregnancy, but the labor
contractions were more frequent and of shorter duration. The contraction phase exceeded the relaxation phase even more so than in early pregnancy.

In early labor the contraction waves were highly uncoordinated and there were multiple peaks and troughs. As activity increased there were the same complex waves but the troughs dipped more and more toward complete relaxation and eventually become the simple and coordinated waves of true labor.

They concluded that in early pregnancy there was a high degree of incoordination of the waves and hence inability to empty the uterus. In mid-pregnancy there was a high degree of coordination, but the amplitude and frequency were not great enough to evacuate the uterus. In labor, there were coordinated, high amplitude and high frequency contractions which could efficiently evacuate the uterus.

External Tocography in Women

Schaffer in 1896, cited by Harris and Gillespie (47), was the first to record contractions of the uterus over the surface of the abdomen. He used an air-containing balloon attached to a "gasometer." The balloon was applied to the abdominal wall over the uterus.
The instruments used have been modified in many ways since Schaffer's first report. Fabre, cited by Harris and Gillespie (47), used a button on the abdomen which pressed against a spring attached to an air pressure device. Rubsamen, cited by Harris and Gillespie (47) and Dodek (35), used a weight suspended on the abdomen and attached to the recorder by a series of strings, pulleys and levers. Needless to say, the apparatus required the patient to lie very still and was subject to many variations due to movement.

Dodek (35) used a fixed plunger and diaphragm of a closed air system which was fixed to the abdomen of the patient. Each contraction caused compression of the air in the system which in turn affected a sensitive rubber tambour. He stated that external tocography is based on the change in antero-posterior diameter of the uterus and maternal abdomen, with contraction of the uterus. The more severe the contraction the greater the change.

Frey, cited by Reynolds (90), used a self-contained "hysterotonograph." Contractions were picked up by a system of rods and gears and transmitted to a recording device. He pioneered the study of longitudinal contraction patterns by using two of these instruments, one over the corpus and one over the isthmus.
Pregnancy was divided into three periods: (1) The quiescent period which is characterized by almost complete inactivity. This period ended about six weeks prepartum. (2) The period of nonrhythmic activity which was characterized by an increase in uterine irritability. During this period there were variable periods of quiescence and activity. (3) The period of rhythmic activity which was characterized by an abrupt or gradual onset of rhythmic contractions which were longer and stronger. The contractions in the last period became the contractions of labor.

Reynolds et al. (91) first described the strain gauge tokodynamometer. In a later paper (92) they gave the details of the apparatus. It consisted of strain gauges applied to the abdomen of the patient with adhesive tape. The gauges were connected to a power supply and recorder. In 1948 (93) they published the first results of the use of the tokodynamometer. In 1954 (90) they published a book on the use of the tokodynamometer and detailed results of their studies. They divided the abdomen into nine different areas and recorded from three of these areas at the same time.

Throughout most of pregnancy the contractions were of a minor nature and intensely localized. In the second half
Lorand, cited by Reynolds (30), introduced a self-contained device held in place by a belt around the patient's abdomen. The receptor was a button maintained in place by a spring arm and the record played out like a ticker tape.

Vignes et al., cited by Reynolds (30), developed a hand-held device which consisted of a lever attached to an indicator scale by a spring.

Rech, cited by Harris and Gillespie (47) and Reynolds (30), was the first to use a transducer. This eliminated the use of an inefficient air or water system and thus increased the accuracy. The writing device could be placed at a convenient distance away from the patient.

Fenning (37, 33) used a system of levers supported by a stand next to the patient. The instrument amplified the contractions four times actual size.

Murphy (37) reported the use of the Lorand tocograph. The activity consisted of: (1) extra-uterine activity such as coughing, sneezing, or movements of the body as a whole; (2) movements of fetal extremities which produced sharp deflections easily distinguished from uterine contractions; (3) changes in the position of the fetal body which produced a shift in the base line; and (4) uterine contractions.
there was a tendency for major contractions to develop. The Braxton-Hicks contractions involved a large part of the myometrium but lacked a high degree of coordination. Mechanical stimulation, such as movements of the fetus, sometimes induced a major contraction arising from the site of the stimulus. As term approached increasing irritability of the uterus and increased coordination of the contractions occurred.

Prior to labor the Braxton-Hicks contractions occurred most often in the fundus of the uterus. As pregnancy progressed the force of the contractions in the fundus increased while the force of those in the lower portion did not change. The duration increased from 110 seconds to 125 seconds in the fundus and from 100 seconds to 110 seconds in the lower portion.

The uterine activity usually occurred in irregular periods, sometimes lasting for only one or two contractions, and sometimes a dozen or more contractions in a period of an hour or more. Between these active periods there were periods of almost complete quiescence.

During labor there was a progressive increase in intensity and duration of the contractions in the fundus. In the mid-uterus there was a slight, but significant
increase in intensity of the contractions. In the lower portion the activity decreased until it disappeared.

In primiparas the intensity of the contractions tended to be greater, while the duration was greater in the multiparas. This may have made the multiparas more efficient in dilating the cervix.

There were three factors affecting dilation of the cervix, intensity, coordination and fundal dominance. If all three of these were good, labor was short.

Delson et al. (32) used a similar two-channel strain gauge tokodynamometer. Their data essentially agreed with that of Reynolds and his co-workers. There was fundal dominance with no significant activity in the lower segment of the uterus. The gradient of activity from fundus to lower segment tended to become greater as labor progressed.

Karlson (63) introduced the use of a granular carbon microphone to record changes of pressure in the uterus. It was based on the principle that the electrical resistance of the carbon changes under varying pressures. The microphone was inserted into the uterus through the cervix. Records were made from various parts of the pregnant human uterus to determine if the pressure is transmitted equally
self-contained with a battery and switch. It was cylindrical, 9 mm. in diameter, and 19.3 mm. long. The whole transmitter was sealed in "Perspex." The transmitter was inserted into the uterus and as the pressure changed the frequency changed. The radio waves were received by a nearby receiver and passed to a chart recorder. Fetal and maternal heart sounds could be eliminated, to some extent, by use of a frequency discriminator.

Another technique for recording the mechanical activity of the uterus was introduced by Kornmesser and Nyboer (66). They recorded the change in electrical impedance to radio frequency currents. There were two electrodes, one at the top of the fundus and one at the bottom, approximately 10 cm. apart. The changes in impedance were probably due to changes in the volume of the uterus, changes in the thickness or bulk of the uterine muscle, fetal movements, amnionic fluid, or variations in blood flow during a uterine contraction.
to all parts of the uterine cavity. There was complete
dissociation of the curves from the fundus, lower segment,
and cervix.

In 1943 Karlson (64) reported his results in more
detail. At the beginning of labor, isolated, incoordinated
contractions were common; as labor progressed the tendency
for coordination appeared and then synchronous contractions
began to appear. At delivery, the contractions were co­
ordinated to form a peristaltic pattern.

Kelly (65) used three carbon granule microphones on a
rod so that one was in the fundus, one in the isthmus and
one in the cervix. Records were made on pregnant women in
the tenth to twenty-fourth week of gestation. Twenty-five
per cent of these women had quiescent uteri. In the others
there were two types of activity. There were small
amplitude, short duration (2 to 4 seconds), high frequency
(one per 3 to 6 seconds) contractions superimposed on high
tonus. This was similar in the fundus and isthmus. The
other type consisted of synchronous fundal and isthmic
contractions. They lasted 30 to 60 seconds and occurred
every 2 to 3 minutes. Tonus was usually absent or slight.

Smyth and Wolff (37) introduced a wireless,
transistorized radio-frequency transmitter which was
MATERIALS AND METHODS

Sheep were chosen as the experimental animals because they usually have only one fetus in each uterine horn and because the uterus with a cotyledonary type placenta has not been studied to any extent. They are relatively inexpensive to purchase and maintain, require little space, and are easy to handle and restrain.

The sheep were purchased from dealers and at livestock auction sales. Table I gives the breed, approximate age, approximate weight, condition and the number of fetuses in the uterus.

On receipt of the ewes they were given a physical examination and the stage of gestation was estimated. The first two sheep were operated on too late in the gestation period and they lambed within two to three days after surgery. The records from sheep number four indicated that there was some irritation due to the manipulation of the uterus and to the sutures. This irritation subsided in seven to eight days. On the basis of this experience it was decided to operate each ewe approximately three weeks prior to parturition. This interval provided time for
Table 1

Description of Animals

<table>
<thead>
<tr>
<th>Sheep No.</th>
<th>Breed</th>
<th>Age</th>
<th>Condition</th>
<th>Approximate Weight (lbs.)</th>
<th>No. of Fetuses</th>
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</thead>
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<tr>
<td>2</td>
<td>Shropshire cross</td>
<td>Aged</td>
<td>Good</td>
<td>100-125</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>Shropshire cross</td>
<td>Aged</td>
<td>Good</td>
<td>100-125</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>Dorset</td>
<td>Aged</td>
<td>Good</td>
<td>175</td>
<td>2</td>
</tr>
<tr>
<td>5</td>
<td>Dorset</td>
<td>Aged</td>
<td>Good</td>
<td>175</td>
<td>2</td>
</tr>
<tr>
<td>6</td>
<td>Shropshire</td>
<td>Aged</td>
<td>Good</td>
<td>125</td>
<td>2</td>
</tr>
<tr>
<td>7</td>
<td>Shropshire</td>
<td>Aged</td>
<td>Good</td>
<td>125</td>
<td>2</td>
</tr>
<tr>
<td>8</td>
<td>Shropshire</td>
<td>Aged</td>
<td>Good</td>
<td>125</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>Oxford</td>
<td>1 yr.</td>
<td>Excel.</td>
<td>175</td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td>Shropshire</td>
<td>1 yr.</td>
<td>Excel.</td>
<td>150</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>Oxford</td>
<td>1 yr.</td>
<td>Excel.</td>
<td>175</td>
<td>2</td>
</tr>
<tr>
<td>12</td>
<td>Corriedale cross</td>
<td>Aged</td>
<td>Good</td>
<td>150</td>
<td>2</td>
</tr>
<tr>
<td>13</td>
<td>Corriedale cross</td>
<td>Aged</td>
<td>Good</td>
<td>175</td>
<td>2</td>
</tr>
<tr>
<td>14</td>
<td>Corriedale cross</td>
<td>Aged</td>
<td>Good</td>
<td>150</td>
<td>2</td>
</tr>
<tr>
<td>15</td>
<td>Suffolk cross</td>
<td>Aged</td>
<td>Poor</td>
<td>100</td>
<td>1</td>
</tr>
</tbody>
</table>
recovery from the surgery and for the irritation to subside before prepartum recordings were made.

**Materials**

Bipolar differential electrodes were used to record the electrical activity. They were made of 0.009-inch diameter silver wire. The base of the electrode, which was sutured to the uterus, was a 2.0 cm. by 2.0 cm. square of Prox Plast™ mesh. This is an inert polyester screen. The wire was tied to one strand of the mesh near the center of the square and the short end put through an adjacent hole. The other wire was attached in the same manner and its short end put through a hole next to the first one, so that the two wires were approximately 1.0 mm. apart. The wires were covered with polyethylene tubing, 0.36 mm. inside diameter by 1.52 mm. outside diameter. Figure 1 D shows an electrode at this stage of construction. The base of the electrodes and the first 3.0 to 5.0 cm. of the insulated wire were covered with Silastic RTV 502, a biologically inert, fluid, silicone rubber which vulcanizes at room temperature. This sealed the wire from body fluids

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2. Dow Corning Corporation, Midland, Michigan.
Figure 1. Bipolar Differential Electrodes

A. Top view of an electrode with the wires attached parallel to the base.

B. Bottom view of an electrode with the wires attached parallel to the base.

C. Side view of an electrode with the wires attached perpendicular to the base. Note the points protruding from the surface.

D. An electrode before covering with Silastic.
and acted as an electrical insulator. A corner or corners were cut off the base of the electrode to identify individual electrodes in a group of four. The external ends of the leads were correspondingly marked with red nail polish.

The electrodes were first made so that the wires came off at right angles to the base and later so that they came off parallel to the base. This made it easier to attach the electrodes to the uterus. Figure 1 A, B and C illustrate three electrodes of this type. Figure 2 is a close-up view of one electrode showing the arrangement of the ends of the wires. The wire on the left is not a part of the electrode assembly, but is a fixation loop covered with a thin layer of Silastic.

Other electrodes used consisted of a series of four pairs of points mounted on one base. Figure 3 shows two such electrodes with the points arranged in linearly. These were used to determine the direction of conduction and speed of conduction of the electrical potentials.

To record contractions of the myometrium, strain gauge arches were used. At first Brodie (10) arches were used, but they did not function after the first two to three weeks in the animal. Figure 4 illustrates a Brodie arch before and after covering with Silastic. The lead wires were covered with polyethylene tubing.
Figure 2. Enlarged Bottom View of One Electrode

Note the arrangement of the points protruding from the base.
Figure 3. Electrode Assembly with Four Bipolar Differential Electrodes Arranged Linearly
Figure 4. Brodie Strain Gauge Arches Before and After Covering with Silastic
Other arches used consisted of Baldwin-Lima-Hamilton\textsuperscript{3} 3R-4, type A-1 strain gauges bonded to an arch made of a strip of 0.012-inch by 0.313-inch stainless steel spring stock. The arch was reinforced with another thickness of the stock soldered to the bottom to limit the distortion of the strain gauge. Silver lead wires were attached to the gauge and covered with polyethylene tubing. The arch and the first 3.0 to 5.0 cm. of the lead wires were covered with Silastic. Figure 5 illustrates this type of arch.

Intrauterine balloons were used to record changes in intrauterine pressure. These were made by sealing the ends of a small cuff for an endotracheal catheter. Clay-Adams\textsuperscript{4} PE 240 polyethylene tubing was inserted in the short tube attached to the cuff and tied on with silk suture. The balloon and part of the tubing was coated with Silastic. The balloon was filled with saline by alternately injecting and aspirating until all of the air was worked out of the balloon and tube. The end of the tube was heat sealed. Figure 6 shows a balloon before and after covering with Silastic.

Late in the experiment, small balloons were inserted into the uterine wall to record local contractions. These

\textsuperscript{3}Baldwin-Lima-Hamilton Corporation, Waltham, Mass.

\textsuperscript{4}Clay-Adams, Incorporated, New York.
Figure 5. SR-4 Strain Gauges Bonded to a Stainless Steel Arch Before and After Covering with Silastic
Figure 6. Intrauterine Balloons Before and After Covering with Silastic
were made from Clay-Adams PE 50 polyethylene tubing, which is 0.53 mm. inside diameter and 0.965 mm. outside diameter. A three-foot piece of the tubing was heat sealed at one end. Gentle air pressure was applied to the inside of the tube while an area close to the seal was rotated and gently heated. Usually after two or three attempts a small distended area could be blown in the end of the tube. The seal was cut off and the tube and balloon filled with water. Both ends of the tube were then sealed. Figure 7 illustrates two balloons of this type.

All of the above equipment was sterilized by soaking in a 1:500 quaternary ammonia, Roccal, solution for 24 hours. Just prior to surgery they were rinsed in sterile water.

Surgical Procedure

Food was withheld from some of the ewes for 24 hours prior to surgery to limit the volume of the abdominal contents. This was not possible in all of the sheep.

Winthrop Laboratories, New York, New York.
Figure 7. Microballoons Used for Insertion into the Uterine Wall
Presurgical preparation consisted of clipping and shaving the operative sites. The sites were scrubbed three times with Phisohex, and then 70 per cent alcohol and Tincture of Metaphen were applied.

Anesthesia was attained using two per cent procaine hydrochloride with epinephrine 1:1000 and 150 units of hyaluronidase per 100 cc. by local infiltration along the line of the incision.

Two sites were prepared. The first was an area 4 inches by 4 inches over the right thorax approximately 6 inches off the midline, where the incision was made to bring the wires to the surface. The second, for the abdominal incision, was in the right flank area.

The abdominal incision was made approximately 10 inches long, parallel to, and 3 to 5 inches posterior to, the last rib in the lower right abdominal wall. The incision sites are illustrated by Figure 3.

The gravid horn of the uterus was brought through the incision and the tip of the uterus exposed. The electrodes were sutured to the uterus with continuous 0.30 mm. Vetafil sutures around the base of the electrode.

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6 Winthrop Laboratories, New York, New York.
3 Bengen and Company, Hannover, Western Germany.
Figure 3. Incision Sites and Fixation of Lead Wires and Tubing on the Body

A. Abdominal incision site.

B. Incision to bring wires and tubing to surface.

C. Tubing from intrauterine balloons with cannula in place.

D. Plugs to connect electrodes and strain gauges to recorder.

Note fixation of the wires and tubing with adhesive tape.
The wires were sometimes sutured to the uterus with simple interrupted Vetafil sutures at some point distant to the electrode to take the strain off the electrode proper. The strain gauges were sutured to the uterus with two simple interrupted Vetafil sutures through each hole in the legs of the arches.

The intrauterine balloon was inserted into the uterus through an incision just large enough to accept the balloon. The allantois-chorion was carefully separated from the uterine wall and the balloon inserted between the membranes and the wall. The incision was closed with continuous inverting Lambert Vetafil suture. The tube was sutured to the uterus with a simple interrupted Vetafil suture about 4 to 6 inches away from the incision.

Figures 9, 10 and 11 illustrate the electrode assembly with four electrodes (A), single electrodes (E), strain gauge arches (C), intrauterine balloon (D), and micro-balloons (E) in place on the uterus.

The wires and tubes were grouped for identification. The groups of wires and tubes were then tied to a 2-foot piece of five eights-inch umbilical tape, which was tied to an 18-inch long flexible probe. The probe was pushed through the peritoneum and muscles from the inside out, near the dorsal end of the incision and approximately half way
Figure 3. Electrodes and Strain Gauge Arches in Place

A. Electrode assembly with four electrodes.
B. Single electrode.
C. Strain gauge arch.
Figure 10. Electrode, Strain Gauge Arch and Intrauterine Balloon in Place

A. Single electrode.

B. Strain gauge arch.

D. Incision for intrauterine balloon, with the balloon and tubing in place.
Figure 11. Electrodes and Microballoons in Place


E. Microballoon.
between the edge of the incision and the last rib. The probe was then turned and directed anterior and dorsal toward the prepared area over the thorax. When the end of the probe could be identified in the area by an assistant an incision was made over the probe. The probe was withdrawn through this incision and the wires and tubes pulled to the outside with the umbilical tape.

Figures 12 to 19 inclusive schematically illustrate the placement of the electrodes, strain gauge arches and microballoons in the eight sheep which survived the surgery and on which recordings were obtained. The uterus was arbitrarily divided into zones. Zone I is the area closest to the body of the uterus. Zone II is the dorsum of the posterior part of the non-gravid horn. Zone III is the dorsum of the uterus over the anterior part of the area of greatest distention. Zone IV is the area lateral to zone III. Zones V, VI, and VII are the medial, dorsal and lateral zones over the area of greatest distention. Zones VIII and IX are the dorsal and lateral zones over the anterior aspect of the area of greatest distention. Zones X and XI are the anterior tip of the uterus. Zone XI is primarily the small portion nearest the ovary. The intra-uterine balloons were placed just anterior to the fetus, approximately in zone X, the most convenient area.
Figure 12. Location of Electrodes and Strain Gauge Arch in Sheep Number 4

Numerals identify position of electrodes and SG denotes strain gauge arch.
Figure 13. Location of Electrodes and Strain Gauge Arches in Sheep Number 6

Numerals identify position of electrodes and SG denotes strain gauge arch.
Figure 14. Location of Electrodes and Strain Gauge Arches in Sheep Number 7

Numerals identify position of electrodes and SG denotes strain gauge arch.
Figure 15. Location of Electrodes and Strain Gauge Arches in Sheep Number 9

Numerals identify location of electrodes and SG denotes strain gauge arches.
Figure 16. Location of Electrodes and Strain Gauge Arches in Sheep Number 11

Numerals identify position of electrodes and SG denotes strain gauge arch.
Figure 17. Location of Electrodes in Sheep Number 12

Numerals identify position of electrodes.
Figure 13. Location of Electrodes and Microballoons in Sheep Number 13

Numerals identify position of electrodes and MB denotes microballoons.
ANTERIOR SHEEP '15

POSTERIOR POSTERIOR

DORSAL VENTRAL

ANTERIOR

LEFT RIGHT

SHEEP '15

POSTERIOR POSTER
Figure 19. Location of Electrodes and Microballoons in Sheep Number 14

Numerals identify position of electrodes and MB denotes microballoons.
The incision in the peritoneum, muscles and fascia was closed with continuous number one chromic catgut sutures. The skin incision was closed with a continuous 0.60 mm. Vetafil suture.

Adhesive tape was placed around the thorax and over the wires and tubes to hold them in place until the sheep had recovered from the surgery.

Postoperative care consisted of 1,000,000 units of penicillin and 2.5 gm. Streptomycin given intramuscularly daily for five days. Most of the ewes were very depressed the first day after surgery, and 1,000 ml. of five per cent dextrose solution were given intravenously. A wound dressing powder containing neomycin sulfate, sulfathiazole, and sulfanilamide was applied to the incision sites daily. The skin sutures were removed in seven to 10 days.

One week postoperative the tape was removed and the wires were soldered to a 2.3 cm. by 3.0 cm. by 3.0 cm. 12-point Cinch-Jones⁹ socket. The sealed ends of the tubing were cut off and an appropriate size cannula was inserted and plugged. The wires, plug, and tubes were taped to the center of the back with adhesive tape around the thorax.

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Figure 8 illustrates the method of fastening the plugs, wires and tubing. Figure 20 illustrates a sheep one week postoperative, ready for recording.

Instrumentation

A Sanborn¹⁰ Poly-Beam recording system, Model 550 M was used to record the electrical and mechanical activity. This system contained a Sanborn Viscoscope, model 569A with electronic switch model 579A, which was used to monitor any four of the eight channels simultaneously.

The preamplifiers were ECG model 350-1600. They are push-pull or single-ended amplifiers. The condenser coupled input was used to amplify the electrical events since it is 50 times more sensitive than the direct coupled side of the amplifier. The frequency response was flat from one ops. (cycles per second) to 50 per cent response at 120 ops. The calibration signal was a standard 1.0 mv. or 0.2 mv. signal inserted in the recording at least once during each recording session. The amplification was adjusted so that 1.0 mv. equaled either 3.0 or 4.0 cm. on the record.

One carrier preamplifier, model 350-3000 B, was used to record changes in intrauterine pressure. The calibration

¹⁰Sanborn Company, Waltham, Massachusetts.
Figure 20. A Sheep One Week After Surgery
signal was an electrical calibration voltage equal to the voltage caused by a known calibration pressure on the transducer. The calibration used was 20 mm. Hg to produce a 40 mm. deflection on the record. A Sanborn pressure transducer model 267, zero to 75 cm. Hg, was used with this preamplifier. The recordings were made with the frequency response selector on average. At this setting frequencies greater than one cps. were averaged and expressed on the record as the average for that time.

Two carrier preamplifiers, model 350-1100 B, were used to record contractions. Three arms of a Wheatstone bridge were assembled in a small chassis and connected to the preamplifiers by a cable. The variable arm of the bridge was the strain gauge in the sheep. The preamplifier amplified the current flow caused by unbalance in the bridge.

A Statham\textsuperscript{11} model P 23, zero to 75 cm. Hg, physiological pressure transducer was used with the above preamplifier and the microballoons.

Respirations were recorded during parturition with the Statham pressure transducer, the carrier preamplifier and a pneumograph placed around the abdomen of the sheep.

\textsuperscript{11}Statham Instruments, Inc. of Puerto Rico, Hato Rey, Puerto Rico.
The recording system was a mirror galvanometer system with light sensitive paper. Paper speeds available were 1.25, 2.5, 5.0, 10, 25, 50, 100, and 200 mm. per second. Time lines appeared every second at the two slower speeds and at 0.04 seconds at the faster speeds. A millimeter scale was printed over the paper from top to bottom.

Each galvanometer had a trace interrupter and the beams were interrupted periodically, and in order from channel one to channel eight. Each individual trace could be identified on the record.

The paper used was Lino-Writ 2\textsuperscript{12} photorecording paper. It was developed and fixed with Kodak X-ray developer and fixer.

The connecting cable was two, six-conductor shielded cables taped together. A 2.3 cm. by 3.0 cm. by 3.0 cm. 12-point Cinch-Jones plug was attached to one end and a small junction box to the other end of the cable. Two wires and the shielding were connected at the box to a two-conductor shielded cable which had a phone jack on the other end. Figure 21 illustrates the Polybeam with the connecting cable attached to the sheep and to the preamplifiers.

\textsuperscript{12}E. I. du Pont de Nemours and Co. (Inc.), Wilmington 98, Delaware.
Figure 21. The Recorder with Connecting Cables Arranged for Recording

A. Pressure transducer attached to the gate.
**Recording Procedures**

The sheep were monitored daily or twice daily for periods of time long enough to record at least two active and quiescent periods. Records were made at 24- or 48-hour intervals, depending on the apparent stage of gestation. When it was apparent that parturition was imminent, monitoring was nearly continuous. Records were made at one- or two-hour intervals for 10 to 20 minutes. Records were made at paper speeds of 1.25 or 2.5 mm. per second, 5 or 10 mm. per second, 25 mm. per second and at 100 mm. per second.

The sheep were loosely restrained by a small gate as illustrated in Figure 22. As they became accustomed to the procedure they were given more freedom so they could lie down.

The pressure transducers were fastened to the gate to reduce artifacts due to movement. They were balanced and filled with water. The plug attached to the cannula in the tubing was removed and a syringe filled with water attached. Any air in the tube was aspirated and replaced with water and the tube attached to the transducer. Some pressure was applied to the microballoons via a three-way valve to be sure the balloon was distended in the tissue.
Figure 22. A Sheep Restrained for Recording

A. Pressure Transducer.
The duration of the active periods and the quiescent periods were measured by monitoring the activity with the viso-scope. They were measured to the nearest minute with a laboratory timer or clock.

**Analysis of Records**

The time prior to parturition was arbitrarily divided into specific time periods as shown in Table 2. Postpartum recordings are denoted as 1:00 postpartum in all graphs and illustrations. The other time periods are denoted by the hour or half hour closest to parturition. For example, "2" on an illustration denotes the period 2:01 to 3:00. Where a recording session fell into two time periods the middle of that session was taken as the point for determining into which of the time periods the data were placed.

The data from each trace were analyzed separately for each time period and later combined with other data where indicated.

The data from zones II, III, and IV; V and VI; and VIII and IX were combined for all the criteria because there were too few electrodes and hence not enough data in some of the zones to make a good comparison. The zones were
Table 2

Division of the Time Prepartum and Postpartum into Specific Time Periods

<table>
<thead>
<tr>
<th>Time Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1:00 hour postpartum to 0:00 (parturition)</td>
</tr>
<tr>
<td>0:01 to 0:30 hours inclusive</td>
</tr>
<tr>
<td>0:31 to 1:00 hours inclusive</td>
</tr>
<tr>
<td>1:01 to 1:30 hours inclusive</td>
</tr>
<tr>
<td>1:31 to 2:00 hours inclusive</td>
</tr>
<tr>
<td>2:01 to 3:00 hours inclusive</td>
</tr>
<tr>
<td>3:01 to 4:00 hours inclusive</td>
</tr>
<tr>
<td>(by 1 hour intervals to 12:00)</td>
</tr>
<tr>
<td>12:01 to 18:00 hours inclusive</td>
</tr>
<tr>
<td>18:01 to 24:00 hours inclusive</td>
</tr>
<tr>
<td>24:01 to 48:59 hours inclusive</td>
</tr>
<tr>
<td>49:00 to 72:59 hours inclusive</td>
</tr>
<tr>
<td>73:00 to 96:00 hours inclusive</td>
</tr>
<tr>
<td>(by 24:00 hour intervals from 96:01 thereon)</td>
</tr>
</tbody>
</table>

combined in a medial to lateral manner so that a comparison can be made between segments of the uterus from posterior to anterior.
Figure 23. Active and Quiescent Periods

The record is from sheep number 12, 18 hours prepartum and was made at a paper speed of 1.25 mm. per second. Strips A and B are continuous. From C to D is 2 minutes. The top four traces are electrical activity. On this record the quiescent period lasted 12.5 minutes and the active period lasted 10.8 minutes.
Electrical Activity

Duration of active and quiescent periods. The active periods consisted of a series of bursts of action potentials. The quiescent period is that interval between two active periods when no electrical activity is recorded. Since these were of long duration, 2 to 8 minutes for the active periods, and 5 to 45 minutes for the quiescent periods, they were measured by monitoring the electrical activity with the viso-scope. Records of a complete cycle of one or more active and quiescent periods were made occasionally. Figure 23 is presented as an example of this.

Frequency of bursts. A burst was considered to be two or more action potentials with no more than 1 second between the end of one potential and the beginning of the next. The total time was taken from the start of one burst to the start of another burst, or from the end of one to the end of another burst. The number of bursts in this time interval was counted and the number of bursts per minute calculated. Usually more than 1 minute was counted, but if short strips were used they were combined to give a more reliable estimate of the frequency. When data from two or more electrodes or time periods were combined the times and numbers of bursts were summed and a new frequency was calculated. Figure 24 illustrates a record with the total time and number of bursts indicated.
Figure 24. Method of Measuring Burst Frequency.

The record is from sheep number 4, 48 hours prepartum and was made at a paper speed of 2.5 mm. per second. The light vertical lines indicate 1-second intervals. The numbers 2, 3, and 4 indicate the trace from the respective electrodes.

a. The beginning of a burst.

b. The end of a burst.

a to b. The duration of a burst.

b to a. The interval between bursts.

a1 to a2. The total time for calculating frequency of the bursts. On this record the time was 69.2 seconds and there were five bursts.

Note the near synchronization of activity between the three traces.
Duration of bursts. The beginning and end of each burst on a record, made at 5.0 mm. per second paper speed or faster, was marked and the time recorded to the nearest 0.2 second. The start of a burst was taken as the first excursion from the base line at the beginning of the first action potential. The end was marked at the return to the base line after the last action potential in the burst. Figure 25 shows three bursts marked for measuring the duration.

A mean and standard deviation were calculated for each electrode in each time period.

Frequency of the action potentials. The action potentials occurred as a series of rapid spike-like complexes. There was usually one large deflection made up of several small deflections. The number of large deflections or complexes were counted for each burst. The frequency was calculated for each burst from the number of action potentials and the duration of that burst.

The frequency recorded for a time period is the mean of the frequencies calculated for each burst in that time period. A standard deviation was calculated for each time period.

Figure 25 illustrates the method of determining action potential frequency.
Figure 25. Method of Measuring the Duration of Bursts, the Interval Between Bursts and the Action Potential Frequency

A record from sheep number 13, 1 hour postpartum, made at a paper speed of 25 mm. per second. The heavy vertical lines indicate 1-second intervals.

a. Beginning of a burst.
b. End of a burst.

a to b. Duration of a burst.
b to a. Interval between bursts.

1. Trace from electrode number 1.
2. Trace from electrode number 4.

The number of action potentials in a burst was counted and divided by the duration of the burst to obtain the action potential frequency. For example, the first burst from electrode number four has a duration of 12.2 seconds and there are 18 potentials in that burst; therefore, the action potential frequency in that burst was 1.48 per second.
Variation of the frequency of action potentials within the bursts. Since Jung (54) and West and Landa (104) have reported a change in the frequency of the action potentials within a burst, it was decided to determine if this occurred in the sheep. Bursts of 10 seconds or more duration were divided into thirds and the number of potentials in each third counted.

The data was combined into three time periods: (1) 24 hours or more prepartum, (2) 0:01 to 24 hours prepartum, and (3) 0:00 to 1 hour postpartum. The data from all the sheep were combined within the above time periods. The t test, as described by Batson (7), for paired data, was used to determine the significance of differences between the first and middle thirds of a burst, the middle and last thirds, and the first and last thirds of the bursts. In all instances where the t test was used in this experiment 0.05 was taken as the significant level of probability.

Interval between bursts. As the duration of the bursts was marked and measured, the intervals were also measured and recorded to the nearest 0.2 second. A mean and standard deviation for each time period was calculated. Figures 24 and 25 illustrate the method of measuring the interval between bursts.
Number of action potentials per five minutes. Five minutes was arbitrarily chosen to express the total number of action potentials in one active period. The following formula was used: 

\[ \overline{D} \times APF \times BF \times 5 = \text{action potentials per 5 minutes} \]

where \( \overline{D} \) is the mean duration of bursts in seconds,

\( APF \) is mean number of action potentials per second,

\( BF \) is the mean number of bursts per minute,

\( 5 \) is the conversion factor for 5 minutes.

This was calculated for each electrode and each time period. When the data from two or more electrodes or time periods were combined, the individual numbers were summed and the new means used in the calculation.

Comparison between two or more areas of the uterus. The uterus was arbitrarily divided into zones as seen in figures 12 to 19. The data from each electrode in a zone and within corresponding time periods were combined and plotted graphically to compare the activity within the various zones.

Conduction time and speed of conduction. Since activity was nearly synchronous at electrodes two, three, and four in sheep number four, the time required for a wave of activity to pass from anterior-posterior direction was
Figure 26. Method of Measuring the Direction of Conduction, Conduction Time Between Electrodes, the Relationship Between Bursts and Contractions, and the Duration of Contractions

The record is from sheep number four, 5 hours prepartum, made at a paper speed of 10 mm. per second. The heavy vertical lines indicate one-second time intervals and the light vertical lines indicate 0.2-second intervals. Numbers 2, 3, and 4 indicate the trace from respective electrodes.

The beginning of the burst at 2a occurred first by 0.4 second, 3a and 4a occurred simultaneously. Therefore, conduction between electrodes two and three was anterior to posterior. The burst at 4 began at electrode 4, .02 second before 3, which was 0.1 second before 2. Therefore, conduction was from posterior to anterior.

The contraction, recorded with the strain gauge, began 0.2 second before the burst at 2a, and 0.6 second before the bursts at 3a and 4a. The second contraction began 1.2 seconds after the burst at 4c, 1.0 seconds after 3c, and 0.9 seconds after 2c. Similarly the ends of the bursts can be related to the peak of the contraction. In this record all of the bursts end before the contraction arrived at its peak, and the time differences can be measured.

The duration of the contraction was from a to c.
compared with the time required for it to pass in a posterior-anterior direction. The time was originally recorded in sequence from the beginning of the first event to the beginning of the second event, and from the second to the third. The time intervals were summed and the direction determined. The only times used were those in which the wave traveled from posterior to anterior or anterior to posterior. The other possible combinations occurred part of the time but were not used in this comparison. It was assumed that the direction of conduction is indicated by the sequence of the beginning of the electrical activity under the electrodes.

The t test for nonpaired data was used to determine the significance of differences in conduction time.

Figure 26 illustrates the relationship between events occurring at electrodes and the method of measuring the time intervals.

Where there were electrode assemblies with four electrodes the speed of conduction was calculated. Records were made at a paper speed of 100 mm. per second and the time required for the wave of activity to pass from one electrode to the next was measured. The time was estimated to the nearest 10 msec. The peak of the initial large deflection was used as the point to measure from whenever
the configuration of the potentials was similar. In some instances the configuration was so irregular or the deflection so gradual that no common point could be found. Figure 27 illustrates a part of a burst with the peaks used, and the time differences marked.

The speed was calculated and expressed as cm. per second. The t Test was used to determine the significance of any differences in anterior to posterior, or posterior to anterior conduction speed. The data were compared in each time period and then combined and the totals compared for each sheep.

**Direction of conduction.** Where there was almost synchronization of individual potentials, such as from the assemblies with multiple electrodes, each potential could be ranked from one to four, with one denoting the potential which occurred first and four the potential which occurred last. Any possible order occurred and the number of times the combination occurred in a time period were recorded. The t Test was used to determine the significance of the difference in the number of times anterior to posterior or posterior to anterior conduction occurred.

Where there was near synchronization of bursts rather than of individual potentials, the comparison was made between the order of the beginning of the bursts, as in sheep number four.
The record is a portion of a burst from sheep number nine, 4 hours prepartum, and was made at a paper speed of 100 mm. per second. The heaviest vertical lines indicate 1-second intervals, the medium vertical lines indicate 0.2 second, and the lightest vertical lines indicate 0.04 second. The top trace was from the most anterior electrode.

The direction of conduction from a to d was anterior to posterior, and from e to h was posterior to anterior. Note the change in direction of the initial large deflection with the change in the direction of conduction.

The time difference was estimated from the peak of the deflection a to peak deflection b as 0.03 second. The time can be similarly estimated for the other potentials. Note the irregular peak at h. No common point can be found between the potentials at g and h to measure the time difference. Therefore, the speed of conduction was necessarily based on the use of clear-cut potentials.
Figure 28. Method of Measuring Amplitude of the Action Potentials

The record is from sheep number four, 1 hour prepartum, and was made at a paper speed of 25 mm. per second. The heavy vertical lines indicate 1-second intervals.

The amplitudes were measured in mm., from peak positive deflection to peak negative deflection. For example, from 1 to 2, 3 to 4, and 5 to 6. Note the 1.0 mv. standard signal inserted on the end of the record.
Figures 26 and 27 illustrate potentials and bursts which can be ranked and the order of beginning activity determined.

**Amplitudes of action potentials.** The amplitudes were measured from the peak positive to the peak negative deflection. The data from all of the time periods were combined for each electrode. The mean and standard deviation was calculated for each electrode and expressed in tabular form. Figure 28 illustrates the method of measuring amplitudes.

**Mechanical Activity**

**Intrauterine pressure.** A sample of four intrauterine balloons were each subjected to pressures up to 100 mm. Hg and the deflections recorded on the polybeam. A calibration curve was drawn from this data. A regression of \( y \) on \( x \) was carried out and the hypotheses of equal slopes for different runs on a given balloon and equal slopes for different balloons were tested. The hypotheses were rejected. From the data for the known pressures a calibration curve with 95 per cent confidence interval was drawn. The predicted variance was 1.675 plus 0.01 \( x^2 \). Figure 29 is the calibration curve for these data.
Figure 29. Calibration Curve for Intrauterine Pressure
In order to combine the data from one time period and obtain a mean and 95 per cent confidence interval for that period the following formula was used:

\[(1) \bar{x} - c \leq m_x \leq \bar{x} + c, \text{ where } c = t_{0.05} \frac{s}{\sqrt{n}}\]

\[x = \text{mm. deflection measured},\]
\[s = \text{standard deviation of } x \text{ for one time period},\]
and \(t\) is obtained from a table of "t" distributions (\(n - 1\) degrees of freedom).

(2) The calibration curve was used to change \(\bar{x}\) to \(\bar{y}\), and \(\bar{x} - c\), \(\bar{x} + c\) into \(c_1\), \(c_2\).

\[(3) d_1 = c_1 - 2 \sqrt{\frac{1.675 + .01}{n} (\bar{x} - c)^2}\]
\[d_2 = c_2 + 2 \sqrt{\frac{1.675 + .01}{n} (\bar{x} + c)^2}\]

(4) Then a 95 per cent confidence interval for \(m_y\) is

\[d_1 \leq m_y \leq d_2\]

The calibration curves and formulas used in calculating the intrauterine pressure are from Whitney (105).

The deflections were measured from the baseline on that particular record, hence intrauterine pressure cannot be considered absolute, but rather the amount of pressure change.

The frequency was calculated from the number of deflections and the total time for the record in the same way as
frequency of bursts. Frequency was expressed in pressure changes per minute. Figure 30 illustrates the points from which the frequency and amplitude of pressure changes were measured.

The change in intrauterine pressure due to straining by the animal was measured from that part of the pressure deflection on which the abdominal pressure was superimposed. Figure 31 illustrates the points from which these measurements were taken.

Contraction recorded with microballoons and strain gauges. The duration of the contractions was measured from the beginning of the deflection to the return to the baseline or the beginning of another deflection. A mean and standard deviation were calculated for each time period.

The frequency of the contractions was measured and calculated the same as for the intrauterine pressure changes. Figures 26 and 32 illustrate the method of obtaining these data.

The contractions were related to electrical activity by measuring the difference in time between the onset of activity under an adjacent electrode or electrodes and the beginning of the contraction. The end of the electrical activity was also related to the peak of the contraction. If the peak was flat, the time was measured from the point
Figure 30. Method of Measuring Intrauterine Pressure and Frequency of Intrauterine Pressure Changes

The record is from sheep number 11, 5 hours prepartum, and was made at paper speed of 5 mm. per second. The light vertical lines indicate 1-second intervals.

The amplitude of the intraperitoneal pressure changes were measured from the baseline at j. Therefore, the amplitudes were measured from b to a point directly below b which corresponds to j, and similarly for e, and h. Note the calibration signal at the end of the record which corresponds to 20 mm. Hg.

There are three pressure changes on this record, from a to c, d to f, and g to i. The time was measured from a to g and the frequency of pressure changes calculated with two pressure changes in this interval.
Figure 31. Method of Measuring the Intrauterine Pressure Change due to the Abdominal Press

The record is from sheep number 12, 0:01 to 1:00 hours prepartum, and was made at a paper speed of 5 mm. per second. The heavy vertical lines indicate 1-second intervals. The top trace is respiration; note the almost perfect synchronization between the abdominal movements and the changes in intrauterine pressure.

The amplitude of the changes were measured from the peak of the pressure change a, and a point directly below the peak on a line between the beginning and end of the sharp deflection, b.
Figure 32. Method of Measuring the Duration and Frequency of Contractions as Recorded with the Micro-balloons, and the Method of Relating the Electrical Activity to the Contractions and the Contractions to Each Other

The record is from sheep number 13, 2 hours prepartum, and was made at a paper speed of 10 mm. per second. The heavy vertical lines indicate 1-second intervals. Four indicates the trace from electrode number four, and mb 1 and mb 2 indicate the trace from the respective microballoons.

The contraction at mb 2a began 0.6 second before the beginning of a burst of potentials at 4a, and 1.2 seconds before the beginning of a contraction at mb 1a. The burst began 0.6 seconds before the contraction at mb 1a. Similarly the relationship between the peak contractions, mb 1b and mb 2b, and the end of the burst, 4b, can be determined. The duration of the contraction is measured from a to c.
where relaxation began. The time was recorded as plus or minus depending on whether the electrical activity was before or after the mechanical. A mean and standard deviation was calculated for these intervals for each time period.

For sheep number 13 the frequency of the order of events was determined for each pair of events, in addition to the time intervals. That is, electrode number four was compared to microballoon number one, microballoon number one was compared to microballoon number two, and electrode number four to microballoon number two. The frequency was determined for each time period. The t Test was used to test the significance of differences between the number of times one event occurred before the other.

Necropsy Examinations

A necropsy was performed on each animal within one week after parturition. The uterus and wires were removed intact and the cable connected to the wires. Continuity and wiring was checked to verify the identity of each trace. The location of each electrode and balloon or strain gauge was described to serve as a check against the descriptions made at surgery. The distances between points of a pair and the distance separating pairs of points were measured.
RESULTS

All of the sheep with the exception of sheep numbers five and eight survived the surgery. Sheep number five died three days following surgery from peritonitis. Sheep number eight died seven days after surgery from a 360-degree torsion of the uterus and accompanying peritonitis. The torsion was apparently caused by twisting the uterus when replacing it into the abdominal cavity during surgery.

Sheep numbers two, three, and 15 lambed within three to four days after surgery and the records were discarded. Sheep number 10 aborted one week after surgery and no records were made.

Records were made from the remaining sheep and are included in the data. All of these sheep had viable lambs, with the exception of sheep number 12 whose lambs were alive at birth but died within 24 hours postpartum, and sheep number 13, whose cervix did not dilate. Records were made from this sheep until the allantois was passed and ruptured. This was taken as the time of parturition. When it was determined, by a vaginal examination, that the cervix had not dilated more than 3.0 cm., the ewe was euthanatized.
Duration of Active and Quiescent Periods

Starting at 49 hours prepartum there appeared to be a slight and gradual decrease in the duration of the active periods. Three to 4 hours prior to parturition there was a marked increase, but this part of the curve was based on too few observations to draw any definite conclusions. Figure 33 illustrates the mean duration with the standard deviation. Since there was no conclusive trend the data for all times was summed and a mean and standard deviation calculated. The mean duration was 6.03 minutes with a standard deviation of 2.16. This represents 327 observations.

The quiescent periods were much more variable, but there was a definite decrease, starting at 18 to 24 hours prepartum. The decrease continued to 10 to 12 hours prepartum, then leveled off at approximately 4 to 7 minutes. In some sheep the quiescent periods disappeared and activity was nearly continuous during the 2-hour period prior to parturition. Figure 34 is a plot of the mean and standard deviation of the duration of the quiescent periods. It shows the variability of the data as well as the definite decrease in duration at 12 to 24 hours prepartum.

There are a few observations which are not included in these data. The intervals in some periods, more than 24
Figure 33. Mean Duration of the Active Periods

Mean duration in minutes and standard deviation plotted against hours before parturition.
MINUTES

HOURS BEFORE PARTURITION

MEAN

STANDARD DEVIATION
Figure 34. Mean Duration of the Quiescent Periods

Mean duration in minutes and standard deviation plotted against hours before parturition.
hours prior to parturition, were occasionally timed at more than 40 minutes. These periods were not used since the total interval was not observed.

**Frequency of Bursts**

The mean burst frequency was four to eight bursts per minute up to 12 to 24 hours prepartum. At 12 to 24 hours prepartum the burst frequency began to decrease to two to four bursts per minute and in most cases the lowest frequencies were recorded during first postpartum hour. Figure 35 illustrates the burst frequency recorded from an electrode in two different sheep. The decrease can be clearly seen in both examples.

Variability was evident in all of the data, but since the time and number of bursts were recorded for each record in a time period and the frequency calculated from the sum of these numbers, no standard deviation was calculated. Since burst frequency is a function of the interval between bursts and the duration of the bursts, this variability can be seen by examining the data describing the interval between bursts and the duration of bursts.

Figure 36 illustrates the combined data for the various zones on the uterus. There is no obvious difference
Figure 35. Mean Bursts per Minute Recorded from Two Electrode Sites

The data from sheep 11 is from electrode number one and that from sheep 12 is from electrode number five. Mean bursts per minute plotted against hours before parturition.
Parturition

HOURS BEFORE PARTUITION

BURSTS PER MINUTE

Sheep No. 11

Sheep No. 12
Figure 36. Mean Number of Bursts per Minute in the Zones

Mean bursts per minute plotted against hours before parturition.
between zones, so they were combined to obtain Figure 37. This graph also clearly shows the decrease in frequency just prior to parturition.

**Duration of the Bursts**

The mean duration of the bursts was between 2 and 6 seconds up to 12 hours prepertum. At 12 hours prepertum, and after the duration of the bursts increased markedly. The durations ranged from 8 to over 20 seconds. Figures 38 and 39 illustrate the mean duration of the bursts and the standard deviation from two electrodes in two sheep. The increase in duration can be clearly seen.

Postpartum there were very few bursts of less than 10 seconds duration. Most of the bursts were 20 to 30 seconds long with many clear-cut spikes in the first part of the burst, and irregular complexes toward the end of the burst.

The data from the zones was not markedly different. Figure 40 gives the mean duration of the bursts for the data from the zones of the uterus.

The mean from all electrodes is given in Figure 41 along with the standard deviation.
Figure 37. Mean Number of Bursts per Minute, All Data Combined

Mean bursts per minute plotted against hours before parturition.
Figure 38. Mean Duration of Bursts from One Electrode Site

The data is from sheep 11, electrode number two. Mean duration of bursts in seconds and standard deviation plotted against hours before parturition.
Mean

Standard Deviation

Seconds

Hours before parturition
Figure 39. Mean Duration of Bursts from One Electrode Site

The data is from sheep 13, electrode number one. Mean duration of bursts in seconds and standard deviation plotted against hours before parturition.
Figure 40. Mean Duration of Bursts in the Zones

Mean duration in seconds plotted against hours before parturition.
Figure 41. Mean Duration of Bursts from Combined Data

Mean duration of bursts in seconds and standard deviation plotted against hours before parturition.
Frequency of Action Potentials

The action potential frequency increased from 1.0 to 1.4 per second in the prepartum period to 1.4 to 1.6 per second starting 10 to 12 hours prepartum. The increase in frequency is not as great as the increase in duration of the bursts. This is illustrated in Figures 42 and 43. Figure 43 illustrates a definite increase in frequency as compared to Figure 42 in which the increase is not so obvious.

The data from the zones of the uterus were similar as seen in Figure 44. The mean and standard deviations for all electrodes are shown in Figure 45.

Variation in Frequency of Action Potentials Within Bursts

The results from comparing the first, middle, and last thirds of bursts of action potentials are presented in Table 3. The difference in number of action potentials in the middle and last thirds from 697 hours to 24:01 hours prepartum was not significant at the 0.05 level. P was greater than 0.05 but less than 0.10. The difference was significant in all the other comparisons.
Figure 42. Mean Frequency of Action Potentials at One Electrode Site

The data is from sheep number 11, electrode number four. Mean frequency in potentials per second and standard deviation plotted against hours before parturition.
Figure 43. Mean Frequency of Action Potentials at One Electrode Site

The data is from sheep number 12, electrode number three. Mean frequency in potentials per second and standard deviation plotted against hours before parturition.
The graph illustrates the change in potentials per second over the hours before parturition, with lines representing the mean and standard deviation. The x-axis represents hours before parturition, while the y-axis shows potentials per second. The graph shows fluctuating trends in potentials as the animal approaches parturition.
Figure 44. Mean Frequency of Action Potentials in the Zones

Mean frequency in potentials per second plotted against hours before parturition.
Figure 45. Mean Frequency of Action Potentials,

Combined Data

Mean frequency in potentials per second and standard deviation plotted against hours before parturition.
It should be noted that in all three time periods the first third had more potentials than did either the middle or last thirds. The difference between the thirds of the bursts was most marked in the postpartum period.

**Interval Between Bursts**

The interval between the bursts of potentials was the most variable of the characteristics of electrical activity. There was a trend toward increased intervals in the last 10 to 12 hours prepartum. The standard deviations were so large that it would be difficult to call this difference significant. It should be noted that for most of the electrodes, the greatest mean intervals occurred between 10 hours prepartum and parturition. Figures 46 and 47 illustrate the data from two electrodes.

There was no apparent difference between the data for the zones of the uterus. This is illustrated in Figure 48. Figure 49 is the combined data for all of the electrodes.

**Number of Action Potentials per Five Minutes**

The number of action potentials per 5 minutes varied from 60 to more than 300. The most obvious characteristic was the variability. In some instances the number of
Table 3
Variation in the Number of Action Potentials in the Middle, Second, and Last Thirds of Bursts

<table>
<thead>
<tr>
<th></th>
<th>Number of Bursts</th>
<th>Number of Potentials</th>
<th>Per Cent in Each Third</th>
</tr>
</thead>
<tbody>
<tr>
<td>697 to 24:01 hours preparrum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First third</td>
<td>95</td>
<td>673.5</td>
<td>34.7</td>
</tr>
<tr>
<td>Second third</td>
<td>95</td>
<td>621</td>
<td>32.0</td>
</tr>
<tr>
<td>Last third</td>
<td>95</td>
<td>644.5</td>
<td>33.2</td>
</tr>
<tr>
<td>Total</td>
<td>95</td>
<td>1939</td>
<td>100.0</td>
</tr>
</tbody>
</table>

|                      |                  |                      |                        |
| 24:01 hours preparrum to parturition |                  |                      |                        |
| First third          | 109              | 939.5                | 35.5                   |
| Second third         | 109              | 882.0                | 33.4                   |
| Last third           | 109              | 821.5                | 31.3                   |
| Total                | 109              | 2643                 | 100.0                  |

|                      |                  |                      |                        |
| Postpartum           |                  |                      |                        |
| First third          | 18               | 261.5                | 47.0                   |
| Second third         | 18               | 173.0                | 31.1                   |
| Last third           | 18               | 121.5                | 21.9                   |
| Total                | 18               | 556                  | 100.0                  |
Figure 46. Mean Interval Between Bursts at One Electrode Site

The data are from sheep number 11, electrode number one. Mean interval in seconds and standard deviation plotted against hours before parturition.
Mean

Standard Deviation

HOURS BEFORE PARTURITION

Parturition
Figure 47. Mean Interval Between Bursts at One Electrode Site

Mean interval in seconds and standard deviation plotted against hours before parturition.
Figure 48. Mean Interval Between Bursts in the Zones

Mean interval in seconds plotted against hours before parturition.
Parturition HOURS BEFORE PARTURITION

SECONDS

Mean
Standard Deviation
Figure 49. Mean Interval Between Bursts, Combined Data

Mean interval in seconds and standard deviation plotted against hours before parturition.
potentials increased from 80 to 100 potentials per 5 minutes to over 300 per 5 minutes in one 24-hour period. In the 2 hours prior to parturition the number of potentials may fluctuate by more than 100 from one hour to the next.

In some of the sheep there was a definite increase in the number of potentials. In others no trend was apparent. In most of the sheep the larger values occurred in the last 12 hours prior to parturition.

Figure 50 shows some of these characteristics for two different electrodes. Figure 51 is the mean for the zones of the uterus, and Figure 52 is the mean and standard deviations for all electrodes.

**Speed of Conduction**

The mean conduction times for sheep number four are presented in Table 4.

The difference between the anterior to posterior and posterior to anterior conduction times are not significant at the 0.05 level.

The conduction speeds for sheep number nine, calculated from the electrode assemblies with four electrodes, are given in Table 5. The difference in speed is significant at the 0.05 level in the 2:01 to 3:00 hours prepartum period, and when the data for all time periods was combined.
HOURS BEFORE PARTUITION

POTENTIALS PER 5 MINUTES

- Sheep No. 12
- Sheep No. 11
Figure 50. Mean Number of Action Potentials per Five Minutes from Separate Electrode Sites

The data from both sheep are from electrode number four. Mean number of potentials per 5 minutes plotted against hours before parturition.
Figure 51. Mean Number of Action Potentials per Five Minutes in the Zones

Mean number of potentials per 5 minutes plotted against hours before parturition.
Figure 52. Mean Number of Action Potentials per Five Minutes, Combined Data

Mean number of potentials per 5 minutes plotted against hours before parturition.
Table 4
Conduction Time (seconds)
Sheep No. Four

<table>
<thead>
<tr>
<th>Time Prepartum</th>
<th>Anterior to Posterior</th>
<th>Posterior to Anterior</th>
<th>No. of Bursts</th>
</tr>
</thead>
<tbody>
<tr>
<td>12:01 to 18:00</td>
<td>1.86</td>
<td>1.57</td>
<td>10</td>
</tr>
<tr>
<td>5:01 to 7:00</td>
<td>1.68</td>
<td>1.43</td>
<td>19</td>
</tr>
<tr>
<td>3:01 to 5:00</td>
<td>0.95</td>
<td>1.76</td>
<td>17</td>
</tr>
<tr>
<td>0:01 to 2:00</td>
<td>2.23</td>
<td>2.74</td>
<td>34</td>
</tr>
<tr>
<td>Mean for all times</td>
<td>1.84</td>
<td>2.01</td>
<td>80</td>
</tr>
</tbody>
</table>

The difference was not significant in the other time periods. The speed was calculated using a distance of 2.5 mm. Two electrodes were used in calculating the speed. The individual points in each electrode were 1.5 mm. apart, and the adjacent electrodes were 1.0 mm. apart.

The number and distribution of measurements within the time periods did not permit comparing the speed within each time period for sheep number 12. The data was combined and one comparison made of all of the data.

The mean speed from anterior to posterior was 12.94 cm. per second and from posterior to anterior it was 11.92 cm.
Table 5
Speed of Conduction
Sheep Number Nine
(cm. per second)

<table>
<thead>
<tr>
<th>Hours Prepartum</th>
<th>Anterior to Posterior</th>
<th>Number of Observations</th>
<th>Posterior to Anterior</th>
<th>Number of Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>313 to 336</td>
<td>6.25</td>
<td>3</td>
<td>9.30</td>
<td>6</td>
</tr>
<tr>
<td>73 to 96</td>
<td>7.50</td>
<td>3</td>
<td>7.96</td>
<td>8</td>
</tr>
<tr>
<td>5:01 to 6:00</td>
<td>3.90</td>
<td>4</td>
<td>6.36</td>
<td>7</td>
</tr>
<tr>
<td>4:01 to 5:00</td>
<td>5.82</td>
<td>15</td>
<td>5.89</td>
<td>20</td>
</tr>
<tr>
<td>2:01 to 3:00</td>
<td>5.00</td>
<td>7</td>
<td>6.94</td>
<td>6</td>
</tr>
<tr>
<td>Postpartum</td>
<td>5.85</td>
<td>15</td>
<td>5.78</td>
<td>11</td>
</tr>
<tr>
<td>Mean for all Time Periods</td>
<td>5.32</td>
<td>57</td>
<td>7.06</td>
<td>67</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sheep No.</th>
<th>Total Bursts or Potentials</th>
<th>Anterior to Posterior</th>
<th>Per Cent</th>
<th>Posterior to Anterior</th>
<th>Per Cent</th>
<th>Other</th>
<th>Per Cent</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>245</td>
<td>56</td>
<td>22.85</td>
<td>99</td>
<td>40.40</td>
<td>90</td>
<td>36.71</td>
</tr>
<tr>
<td>6</td>
<td>412</td>
<td>243</td>
<td>58.98</td>
<td>145</td>
<td>35.20</td>
<td>24</td>
<td>5.82</td>
</tr>
<tr>
<td>9</td>
<td>119</td>
<td>48</td>
<td>40.33</td>
<td>66</td>
<td>55.50</td>
<td>5</td>
<td>4.20</td>
</tr>
<tr>
<td>12</td>
<td>336</td>
<td>132</td>
<td>34.78</td>
<td>204</td>
<td>59.82</td>
<td>Not determined</td>
<td></td>
</tr>
</tbody>
</table>
per second. The value of $t$ was 0.38 for 81 observations. The difference in speeds was not significant at the 0.05 level.

The distance was 4.1 mm. between one pair of electrodes and 5.9 mm. between the other pair.

**Direction of Conduction**

The frequency of anterior to posterior conduction and posterior to anterior conduction is given in Table 6. The frequency of combinations other than posterior to anterior or anterior to posterior are also listed. The data is for all of the time periods combined. The only sheep in which the difference is significant is sheep number four.

**Amplitude of Action Potentials**

The mean, standard deviation and maximum recorded amplitude for each sheep and most of the electrodes are given in Table 7. The mean amplitude was between 0.25 and 0.50 mv. in most cases. The standards deviations are relatively large and adequately express the variability of the amplitudes.
## Table 7

**Amplitude of Action Potentials in Millivolts**

<table>
<thead>
<tr>
<th>Sheep Electrode No.</th>
<th>Number of Potentials Measured</th>
<th>Mean Amplitude</th>
<th>Standard Deviation</th>
<th>Maximum Amplitude Recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>2</td>
<td>0.41</td>
<td>0.16</td>
<td>1.08</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>0.38</td>
<td>0.17</td>
<td>0.93</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>0.53</td>
<td>0.27</td>
<td>1.57</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
<td>0.26</td>
<td>0.12</td>
<td>0.56</td>
</tr>
<tr>
<td>6</td>
<td>3</td>
<td>0.26</td>
<td>0.13</td>
<td>0.64</td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>0.41</td>
<td>0.18</td>
<td>0.93</td>
</tr>
<tr>
<td>6</td>
<td>5</td>
<td>0.22</td>
<td>0.28</td>
<td>0.56</td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>0.44</td>
<td>0.28</td>
<td>2.00</td>
</tr>
<tr>
<td>9</td>
<td>1</td>
<td>0.95</td>
<td>0.49</td>
<td>2.48</td>
</tr>
<tr>
<td>9</td>
<td>3</td>
<td>0.56</td>
<td>0.48</td>
<td>2.61</td>
</tr>
<tr>
<td>11</td>
<td>1</td>
<td>0.27</td>
<td>0.14</td>
<td>0.88</td>
</tr>
<tr>
<td>11</td>
<td>4</td>
<td>0.28</td>
<td>0.19</td>
<td>1.33</td>
</tr>
<tr>
<td>12</td>
<td>1</td>
<td>0.70</td>
<td>0.39</td>
<td>2.08</td>
</tr>
<tr>
<td>12</td>
<td>2</td>
<td>0.29</td>
<td>0.18</td>
<td>1.03</td>
</tr>
<tr>
<td>12</td>
<td>3</td>
<td>0.37</td>
<td>0.23</td>
<td>1.03</td>
</tr>
<tr>
<td>12</td>
<td>4</td>
<td>0.41</td>
<td>0.19</td>
<td>1.25</td>
</tr>
<tr>
<td>12</td>
<td>5</td>
<td>0.35</td>
<td>0.22</td>
<td>1.15</td>
</tr>
<tr>
<td>13</td>
<td>1</td>
<td>0.28</td>
<td>0.15</td>
<td>0.93</td>
</tr>
<tr>
<td>13</td>
<td>3</td>
<td>0.29</td>
<td>0.17</td>
<td>1.15</td>
</tr>
<tr>
<td>13</td>
<td>4</td>
<td>0.34</td>
<td>0.20</td>
<td>1.13</td>
</tr>
<tr>
<td>14</td>
<td>1</td>
<td>0.56</td>
<td>0.35</td>
<td>1.25</td>
</tr>
<tr>
<td>14</td>
<td>2</td>
<td>0.50</td>
<td>0.23</td>
<td>1.05</td>
</tr>
<tr>
<td>14</td>
<td>4</td>
<td>0.45</td>
<td>0.22</td>
<td>1.05</td>
</tr>
<tr>
<td>14</td>
<td>5</td>
<td>0.50</td>
<td>0.21</td>
<td>0.95</td>
</tr>
</tbody>
</table>
Intrauterine Pressure Changes

Pressure changes were first noted in sheep number 11 at 169 hours prepartum, and in sheep numbers nine and 12 at 72 hours prepartum.

The pressure changes averaged between 6 mm. Hg and 30 mm. Hg up to 12 hours before parturition. The pressure changes in sheep number 12 steadily increased to over 100 mm. Hg at parturition. In sheep numbers nine and 11 the changes remained fairly constant from 8 hours prepartum to 2 hours prepartum. There was an abrupt increase at 2 hours prepartum to a mean of 65 mm. Hg in sheep number nine and to over 100 mm. Hg in sheep number 11. The data were particularly variable in the last 10 to 12 hours prior to parturition. Figure 53 gives the means and 95 per cent confidence intervals for sheep numbers nine, 11, and 12.

The frequency of the pressure changes was between 1.5 and 6.5 per minute. The number of the values was too small to detect any definite trend. There appeared to be a slight decrease in frequency starting 12 hours prepartum. The values for sheep numbers nine and 11 were in the same range, but those for sheep number 12 were somewhat less. Figure 54 gives the mean frequency and standard deviation for all three of the above sheep.
PRESSURE (mm. Hg)

Mean — — Standard Deviation

Sheep No. 9

Sheep No. 11

Sheep No. 12

HOURS BEFORE PARTURITION

> 100

205
Figure 53. Mean Amplitude of Intrauterine Pressure Changes

Mean amplitude in mm. Hg with standard deviations plotted against hours before parturition.
Figure 54. Mean Frequency of Intrauterine Pressure Changes

Mean changes per minute plotted against hours before parturition.
CHANGES PER MINUTE

HOURS BEFORE PARTURITION

Parturition

160
121
80
40
20
10
6
4
3
2
1

Sheep No. 12

Sheep No. 11

Sheep No. 9
range for both sheep number four and sheep number 13. There was a definite decrease in frequency starting 12 to 24 hours prepartum. The frequency averaged 2.5 to 5.0 contractions per minute up to 24 hours prepartum. The frequency gradually decreased to 2.0 contractions per minute at 0:00 to 1 hour postpartum. Figure 55 illustrates the mean frequency with the standard deviations for sheep number four, as recorded with the strain gauge arches, and for sheep number 13 as recorded with the microballoons.

The duration of the contractions began increasing from a mean of 9 to 13 seconds, at 12 to 24 hours prepartum, to 22 to 24 seconds just prior to parturition and in the first hour postpartum. Figure 56 illustrates the mean duration and standard deviation of the contractions for sheep numbers four and 13.

**Relationship Between Contractions and Electrical Activity**

There was almost complete synchronization of the onset of electrical activity under all three electrodes with the onset of contractions in sheep number four to the extent that all events began within the same short time interval. There was no constant order of events or time intervals
The pressure changes due to straining by the sheep increased from 27 mm. Hg at 4:01 to 5:00 hours prepartum, to 48 mm. Hg, at 0:01 to 0:30 hours prepartum, for sheep number 12. The mean change due to straining in sheep number nine was 96 mm. Hg at 0:01 to 0:30 hours prepartum. Table 8 gives the mean and 95 per cent confidence intervals for the above values.

Table 8
Pressure Changes Induced by Straining

<table>
<thead>
<tr>
<th>Sheep No.</th>
<th>Hours Prepartum</th>
<th>Mean (mm. Hg)</th>
<th>95 per cent Confidence Interval</th>
<th>Number of Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
<td>4:01 to 5:00</td>
<td>27</td>
<td>19.57 to 37.4</td>
<td>39</td>
</tr>
<tr>
<td>12</td>
<td>0:31 to 1:00</td>
<td>40.5</td>
<td>32.11 to 49.40</td>
<td>32</td>
</tr>
<tr>
<td>12</td>
<td>0:01 to 0:30</td>
<td>48</td>
<td>36.72 to 59.70</td>
<td>8</td>
</tr>
<tr>
<td>9</td>
<td>0:01 to 0:30</td>
<td>96</td>
<td>77.3 to 100</td>
<td>38</td>
</tr>
</tbody>
</table>

Contractions Recorded with the Microballoons and Strain Gauge Arches

Out of nine strain gauge arches in five sheep only one functioned satisfactorily for a significant interval of time. The frequency of the contractions was in the same
CONTRACTIONS PER MINUTE

HOURS BEFORE PARTURITION

Sheep No. 13
Mb. No. 2

Sheep No. 1
Mb. No. 1

Sheep No. 4
Figure 55. Mean Frequency of Contractions as Recorded
with the Microballoons and Strain Gauge Arches

Mean frequency in contractions per minute plotted
against hours before parturition.
Figure 56. Mean Duration of Contractions as Recorded with Microballoons and Strain Gauge Arches

Mean duration in seconds and standard deviation plotted against hours before parturition.
between events. The same relationship is present between the end of the electrical activity and the peak of the contraction. Figure 57 illustrates these relationships.

The electrical activity under electrode number four in sheep number 13 began most often before the contractions. The mean interval between the electrical and mechanical events varied from less than 1 second to 6 seconds. This is illustrated in Figure 58. The difference between the number of times the electrical activity occurred first and the mechanical activity first was significant at the 0.05 level.

There was no significant difference between the number of times the electrical activity ended before the peak of the contraction and the number of times it ended after the peak of the contraction.

There was no significant difference between the onset of the contraction at microballoon number one and at microballoon number two, or between the peaks of the contractions at the two balloons. Figure 58 illustrates these relationships for sheep number 13.
Figure 57. Relationship of the Electrical Activity to Contractions in Sheep Number Four

The top figure is the relationship of the beginning of the bursts of electrical activity to the beginning of the contraction. The bottom figure is the relationship of the end of the bursts to the peak of the contraction.

The numbers under the bars denote the order of events. The difference in the height of the bars in a group of bars denotes the time interval separating individual events.
Figure 58. Relationship of the Electrical Activity to Contractions in Sheep Number 13

The top figure is the relationship of the beginning of the bursts of electrical activity to the beginning of the contraction. The bottom figure is the relationship of the end of the bursts to the peak of the contraction.

The numbers under the bars denote the mean order of events as determined from the mean time intervals between the electrical and mechanical events. The space between the tops of the bars on the vertical axis denotes the mean time interval between events. The dotted lines above the bars denotes the standard deviation. Since the electrical activity was taken as zero and the intervals measured from that point, there is no standard deviation for the contraction.
DISCUSSION OF RESULTS AND CONCLUSIONS

The periodicity of the electrical activity noted in this experiment has not been described as such in any other species. This may not be present in other species or it may have been masked by irritation from handling the tissues in acute experiments. Very few chronic experiments have been performed. Kao (62) and Daniel and Renner (30), in in vivo experiments on rabbits and cats respectively, did not report any periodicity, although they did note a lack of spontaneous activity until just prior to parturition.

The mechanism for this periodicity in sheep can only be guessed at. It may be an inherent biological rhythm modified by neural or endocrine factors. The decrease in interval between active periods accompanies the increase in action potential frequency in the bursts and duration of the bursts. Hence, it appears that the periodicity of the electrical activity is under the influence of the same factors which modify the other characteristics of electrical activity.

The frequency of the action potentials for the sheep falls within the reported range of one to two per second for
other species (5, 44, 58, 59, 62, 68, 71, 101, 109, 110). Higher frequencies of four to nine potentials per second have been reported in the rat and cat (43, 57).

The increase in frequency of the potentials toward parturition is an indication of the increased overall mechanical and electrical activity of the uterus.

Although the amplitudes were measured, no attempt was made to relate them to parturition because they were affected by too many extrinsic factors. Nearly all of the electrodes were pushed away from the myometrium. On necropsy there was usually a layer of fibrin between the electrode and the serosa of the uterus. In some cases the electrodes were tipped away from the uterus, apparently due to pressure on the electrodes from the abdominal wall or viscera.

The amplitudes recorded from the sheep agree closely with reports on other species where similar electrodes were used (5, 28, 29, 30, 31, 55, 61, 62). If the extrinsic factors could be eliminated, it would be of value to determine if there is any change in amplitude with impending parturition.

The duration of the bursts was somewhat shorter than the 20- to 60-second durations reported for other species (30, 43, 55, 101, 104). The marked difference may be in the
definition of a burst. Kao (62) reported a frequency of 3.5 action potentials per minute, and called this a burst. The definition of a burst in this experiment did not include such low frequency events. Most of the potentials were grouped in clear-cut bursts and it was not difficult to differentiate a burst from an interval between bursts. There were many periods where there were single potentials more than 1 second apart in the interval between bursts. If these potentials had been included in the burst the durations would have been somewhat longer in many of the time periods. There also were periods, particularly postpartum, where there were two or more distinct bursts of action potentials with many small potentials between. These small potentials were not included as a part of the bursts.

Some of the discrepancies may have been due to irritation of the tissues in acute experiments. The records made in the sheep 7 to 10 days after surgery showed that there was much irregular activity with short bursts of potentials and short intervals between the bursts. This gradually subsided to the level seen later. This same phenomenon occurred regardless of the stage of gestation when the sheep were operated upon.

The variation of the frequency of the action potentials within the bursts does not agree with any other report in
direction other than on the long axis between the electrodes, the time represents the difference in arrival time at the two points. If the wave of potential change approaches at right angles to the line between the two points the measured time could conceivably be zero. Therefore, the time expressed here is a mean which includes the times due to different angles of approach, and the true speed would be somewhat less. In spite of this, the values arrived at are within the range of 8.0 to 12.5 cm. per second reported for other species (28, 29, 31, 42, 68, 83).

The direction of conduction as measured in sheep number four, with the three separate electrodes, was more posterior to anterior. This agrees with the report by Jung in the cat (56). With the electrode assembly of four electrodes, where each electrode was 1.0 to 3.0 mm. apart, there was no difference in direction of conduction. This agrees with Kao (62) on the rabbit. Daniel and Renner (30) in the cat, reported that conduction was more anterior to posterior.

The difference between the sheep was probably due to the distance between the electrodes. No synchronization between single electrodes was apparent in sheep where there was synchronization with the assemblies of four electrodes. Sheep number four had no assembly of four electrodes so no
the literature. In this experiment the frequency was always greater in the first third than in the middle and last thirds of the burst up to parturition. In the period 24 hours prior to parturition, the frequency was greater in the first third than in the other two thirds, and in the postpartum period the first third was markedly greater than the second third and the second third greater than the last third. The reports on other species (44, 57, 59, 72, 80, 104) all recorded an increasing frequency of the action potentials to the middle or the end of the burst, which coincided with the peak of the contraction, and then a decrease to a frequency which was less than in the beginning of the burst.

The interval between the bursts of action potentials was somewhat shorter than the 30- to 60-second intervals reported by Jung (55) and Kuriyama and Csapo (71) in the cat and rat respectively. The striking feature of the intervals was their variability, which emphasizes the randomness of the electrical activity. This was the most variable characteristic of the electrical activity.

The measured conduction speed may not be an accurate measurement of the actual speed with which the potentials were conducted from one electrode to another. If the potentials were approaching the electrodes from any
in part to the use of a faster recording speed which gave a better separation of the small contractions and also to the definition of a contraction. In most of the other reports one contraction was measured from the point the pressure left the baseline to the point where it returned to the baseline. In the sheep an obvious peak, although superimposed on a large deflection was considered one contraction. Hence, these data are somewhat higher.

All of the data can be combined with other information available to form a hypothesis of the activity of the uterus prior to parturition and during parturition.

It is obvious that there is no concise mechanism for initiating or controlling the activity of the pregnant uterus. The presence of the active and quiescent periods and the decrease in the duration of the quiet periods indicates that there is an increase in overall activity in the uterus towards parturition. This increase was apparent in all zones of the uterus which were studied. The question of equal activity in all of the myometrium is still not answered since it was mechanically impossible to place electrodes on the body of the uterus, particularly near the cervix.

The variability of the duration of the intervals between bursts, in particular, suggests the absence of any
comparison between the techniques could be made. Therefore, the results in the sheep are inconclusive. It is significant to note, however, that also there was no difference in the direction of travel of the contractions when the two microballoons in sheep number 13 were compared.

The intrauterine pressures recorded were too few to draw any definite conclusions. The changes in pressure fell within the 30 to 90 mm. Hg reported for the first stage of labor in the human (4, 11, 21, 86, 96, 107, 108, 111). The method of measuring intrauterine pressure did not include the tonus or resting intrauterine pressure. If 4.0 to 5.0 mm. Hg, as recorded by Bienariz and Reynolds (9) for tonus in the sheep, is added to these data there would be no significant change.

As seen from the data, the abdominal movements contribute a significant amount of force to the expulsion of the fetus in the second stage of labor. The values recorded from the sheep, although very variable, are approximately equal to those reported in the human (11, 79, 107, 108).

The frequency of the intrauterine pressure changes are somewhat greater than the less than one per minute reported for humans (2, 4, 11, 21, 23, 79, 86, 95). This may be due
Neural connections may be of significance. Jung (56) showed that by mechanical stimulation of the cervix a burst of action potentials would result and be conducted over part of the uterus. However, in the absence of neural connections, spontaneous activity is still present, as shown by the many experiments on isolated pieces of myometrium.

The lack of synchronization of the electrical activity between areas of the uterus also indicates a lack of a central or overall controlling mechanism. There was some synchronization noted in one sheep, but even in this case there was no constant relationship between events under the three electrodes. Others have noted synchronization of bursts over limited areas (28, 56, 72) but none over the distances described here. This synchronization never occurred in any other of the sheep. This may have been due to chance placement of the electrodes. There was synchronization of the potentials over short distances as recorded with the electrode assemblies of four electrodes close together, indicating that small areas of the myometrium are active simultaneously. This agrees with what other people have found in other species. West and Landa (104) noted that two cells close together were not always active simultaneously. Landa, et al. (72), noted no
rhythmical controlling mechanism. The refractory period of the cells certainly regulates the interval to some extent. Jung (56) showed that there was a relative refractory period of 15 to 30 seconds after the end of a burst of action potentials before another burst could be elicited by stimulation of the cervix of the cat. Bozler (14) described an absolute refractory period of 10 to 60 seconds, and a relative refractory period of several minutes in the uterus of several species. Therefore, there apparently is a period following the burst of action potentials when the uterus will not respond, as well as a much shorter refractory period following each action potential.

The bursts can be initiated or controlled by many factors. Some workers have concluded that stretch is an important factor in the initiation of bursts of action potentials and in the conduction of the potentials. Daniels (29), West and Landa (104), and Landa, et al. (72), demonstrated that stretch would initiate a burst of action potentials as well as a contraction. Therefore, a mechanical stimulus, such as maternal or fetal movements may initiate electrical activity. Activity may be conducted from one area to another by stretch. As one area contracts, another adjacent area is stretched, stimulating electrical activity in that area. Stretch may facilitate the conduction of action potentials.
The contractions of the myometrium are regulated by the electrical activity. Jung (57), Kuriyama (68), and Marshall and Katsh (82) reported that the strength of the contraction is regulated by the number of active cells, the action potential frequency, and by the duration of the train of action potentials. From this and the observed increase in the duration of the bursts, and the observed increase in action potential frequency towards parturition in sheep, it can be seen that the contractions of the myometrium begin to increase in strength at about 12 to 24 hours prepartum. This continues until it reaches a peak just prior to parturition or at parturition. This is also shown by the increase in amplitude of the intrauterine pressure changes.

It has been shown by many people that the conduction of the electrical activity in the uterus is irregular and usually over very short distances (15, 28, 29, 56, 62, 72, 104). The variability of the data is in agreement with this. Most workers (56, 60, 68, 71, 80, 81) agree that any cell in the myometrium is capable of initiating electrical activity, i.e., may be a pacemaker. This supports the results found here that in most instances there is no predominant direction of conduction. Although others have reported that one end or the other of the uterus is more
conduction beyond 2 cm. and complete dissociation when the electrodes were placed transversely on the uterus. Jung (56) noted that when the electrodes were placed more than 5.4 cm. apart there was some synchronous activity and some independent activity. Kao (62) noted much variability in the electrical activity even in adjacent strips. Marshall (80) concluded that not all fibers contract synchronously, and that a fiber which acts synchronously with neighboring fibers at one instant may not do so at another instant.

Although the electrical and mechanical events in this experiment were not synchronous, it has been very well established that the mechanical events are associated with the electrical activity of the myometrium. West and Landa (104), Landa et al. (72) and Daniel (29) noted complete synchronization of the electrical activity with the mechanical activity under the proper conditions. Landa et al. (72) noted that with large strips there was very little synchronization, but when using small strips there was complete coordination. This is obviously why there was no better coordination in the sheep. In all cases it was mechanically necessary to place the electrodes at least 2 to 8 cm. away from the strain gauges or the microballoons and hence the areas being compared were too far apart.
potential frequency, the duration of the contraction, the amplitude of the intrauterine pressure changes and the duration of the bursts all increased. If all of these factors increase at parturition but without any greater controlled coordination of the activity, the increased efficiency can be explained by the fact that as more fibers are active at any one time and for longer periods of time the probability increases that more and more fibers and hence larger areas of the uterus will be active at any one time. Eventually in the last 2 to 3 hours prepartum a much greater per cent of the myometrium is active simultaneously for longer periods of time and each fiber is developing more tension than in the earlier parts of the gestation period. These observations indicate a coordination of the myometrium without the function of an intrinsic or extrinsic coordinating mechanism. This greater coordination results in increased intrauterine pressure and greater expulsive force.
active. The reports are conflicting, and until more evidence is forthcoming, the results indicate that there is no pacemaker area as such. Hence, the lack of synchronization of activity in different areas of the uterus may be due to the lack of predominant pacemaker areas; lack of an extrinsic controlling mechanism; and failure of conduction over large areas, which may be due to interference by adjacent active areas or lack of an efficient conducting mechanism.

No definite conclusions can be drawn from the evidence at hand but it appears that parturition in the sheep is due to a progressive coordination of the random activity of the myometrium. Early in the prepartum period the characteristics of uterine activity are (1) low irritability, as shown by the greater duration of the quiescent periods and shorter duration of the bursts; (2) low action potential frequency which denotes weaker contractions; and (3) short inefficient contractions as shown by the low intrauterine pressure changes, which in most of the sheep were not measurable prior to 72 hours prepartum, and by the short duration of the bursts. There was no evidence of a special synchronizing mechanism in this period.

Progressively during the period immediately prior to parturition the excitability of the myometrium, the action
SUMMARY

The objectives of this experiment were (1) to describe the electrical activity of the gravid uterus of the sheep, (2) to determine if the electrical activity as monitored is the same in all areas of the uterus, (3) to determine whether there is any predominant direction of conduction, (4) to estimate the speed of conduction and (5) to try to relate the electrical activity to the mechanical activity.

The uterus was arbitrarily divided into zones. Bipolar differential electrodes were placed on the uterus within the zones. Microballoons and strain gauge arches were used to record the mechanical activity of small areas of the myometrium. A balloon inserted between the mucosa and the placenta was used to record changes in intrauterine pressure. The wires and tubing were brought to the outside and recordings were made with as little restraint as possible.

The electrical activity occurred in periods 2 to 3 minutes long. During these periods the activity was not continuous but occurred as bursts of action potentials. A description of the electrical activity was accomplished by measuring the duration of the active and quiescent periods,
the duration of the bursts, the frequency of the bursts, the
duration of the interval between bursts, the frequency of
the action potentials in the bursts, the number of action
potentials per 5 minutes, the variation in frequency of
action potentials within a burst, the amplitude of the
action potentials, and the speed of conduction.

The mean duration of the active periods was 6.03
minutes. The duration decreased slightly beginning 24 hours
prior to parturition. The quiescent periods were variable,
lasting from 10 to 40 minutes except for the 24 hours im-
mediately prior to parturition. At 24 hours prepartum the
duration of the quiescent periods began to decrease. At
parturition the quiescent periods were very short, 1 to 2
minutes, or were not apparent at all.

The duration of the bursts and the frequency of the
action potentials increased, beginning approximately 12 to
24 hours prepartum. The duration of the bursts varied from
1.0 to 20 seconds, with most of the values from 2.0 to 6.0
seconds. There were from 1.0 to 1.6 potentials per second.
The frequency was greater in the first third than in the
last two thirds of the bursts regardless of the time prior
to parturition. There were fewer potentials in the last
third than in the second third of the burst in the period
24 hours prepartum to parturition, and in the first hour
postpartum.
The number of action potentials per 5 minutes was a markedly variable characteristic. In spite of this variability an increase in the number of potentials per 5 minutes could be seen in the 12 hours prior to parturition. The number of potentials varied from 80 to 300 per 5 minutes. Most of the values near parturition were from 150 to 300.

The number of bursts per minute decreased markedly in the 12 to 24 hours prior to parturition. The number decreased from four to eight bursts per minute to two to four per minute.

The interval between bursts was the most variable characteristic of the electrical activity. The intervals ranged from 1.0 to 30 seconds. There was a decrease in the intervals noted in the last 12 hours prior to parturition but the data was so variable that it was difficult to call this trend significant. The amplitude of the action potentials were measured but no attempt was made to relate them to the events of parturition. The amplitudes ranged from 0.1 mv. to 2.60 mv.

The speed of conduction was recorded and calculated to be from 7.0 to 12.0 cm. per second. There was no significant difference between the speeds at different
times prepartum or between the speed of anterior to posterior compared to posterior to anterior conduction.

The direction of conduction was determined by using data from individual potentials recorded from electrode assemblies with four electrodes and from data from almost synchronous bursts recorded from single electrode sites. The data using the individual potentials showed no significant difference in the direction of conduction. The data from the bursts indicated that posterior to anterior conduction occurred most frequently.

The intrauterine pressures ranged between 6 and 30 mm Hg up to approximately 12 hours prior to parturition. In one instance, beginning 12 hours prior to parturition, it steadily increased to over 100 mm Hg. In the other two sheep the pressure showed a slight increase up to 2 hours prepartum, and then a sharp increase to between 70 and 100 mm Hg until parturition. The abdominal press contributed approximately 100 mm Hg pressure intermittently to the expulsive efforts of the uterus in the last few hours prior to parturition. The frequency of the intrauterine pressure changes seemed to decrease as maximal intrauterine pressures increased and with impending parturition.

The number of contractions per minute began to decrease from 2.5 to 5 at 12 hours prepartum to two per minute at
increase the probability that more areas of the myometrium will contract at once. The increased action potential frequency results in increased strength of contractions. Both changes apparently act to increase the intrauterine pressure. The increased pressure serves to dilate the cervix and eventually, with the aid of the abdominal press to expel the fetus.
parturition. The duration increased similarly from approximately 10 seconds to approximately 20 seconds at parturition.

The mechanical and electrical events occurred within the same short interval of time. When the events were compared there was no constant order of events or time intervals between events.

The measurements of nearly all of the characteristics of the electrical activity fell within the range reported by other workers in other species and by other techniques. The periodicity of the active periods has not been described before as such.

The electrical activity of the sheep uterus is characterized by variability, and a change from short ineffective bursts and contractions to longer more efficient contractions with more frequent periods of activity. There apparently is no better synchronization of the electrical or mechanical activity between the large areas of the myometrium studied at parturition than before parturition. There is no evidence of peristaltic-like waves of contraction, but rather an independent or autonomous contraction of many segments of the myometrium. As parturition approaches the increased duration of the bursts tends to
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AUTOBIOGRAPHY

I, Philip William Murdick, was born in Akron, Ohio, November 13, 1928. I received my secondary school education in Stow Township School, Stow, Ohio. The pre-veterinary medical portion of my education was received at The Ohio State University. I was admitted to the College of Veterinary Medicine, The Ohio State University, in the autumn quarter of 1943 and received the Doctor of Veterinary Medicine degree in June 1952. For the next four years I practiced veterinary medicine in Akron, Ohio, and Belle Center, Ohio. I returned to The Ohio State University in May 1956 as an instructor in the Department of Veterinary Medicine and as a graduate student. I received the Master of Science degree in December 1958. I am currently employed as an instructor in the Department of Veterinary Medicine.


