Smooth Muscle Electrical Activity in the Oviduct, and the Effect of Oxytocin, Prostaglandin F₂ₐ, and Prostaglandin E₂ on the Myometrium and the Oviduct of the Cycling Mare

Mats H.T. Troedsson, Irwin K.M. Liu, Michelle Ing, and John Pascoe

Department of Population Health and Reproduction and Department of Surgery and Radiology, School of Veterinary Medicine, University of California, Davis, California 95616

ABSTRACT

Myoelectrical oviductal activity was evaluated during the estrus cycle in the mare using electromyography. The effects of 20 IU oxytocin (i.v.), 10 mg prostaglandin (PG) F₂ₐ (i.m.), and 10 mg PGE₂ (i.m.) on electrical activity of the myometrium and myosalpinx were investigated. Electrodes were surgically implanted in the myosalpinx and in the myometrium of the uterine horn and body. Myoelectrical activity was analyzed for total activity, frequency and duration of activity bursts, intensity, and amplitude. Spontaneous myoelectrical activity of the oviduct was not affected by the stage of the estrous cycle. Significantly more activity was recorded from the myosalpinx than from the myometrium throughout the estrous cycle (57.3 ± 2.7% vs. 28.8 ± 1.6%). All treatments resulted in increased activity in the myometrium and myosalpinx. The duration of the effect was 1 h for oxytocin, 5 h for PGF₂ₐ, and 2 h for PGE₂. Oxytocin and PGF₂ₐ treatment during estrus resulted in an increased number of uterine activity bursts of high intensity and amplitude, whereas these treatments during diestrus, compared to those during estrus, resulted in less frequent uterine activity bursts of longer duration. Characteristics of PGE₂-induced myometrial activity were similar to those of oxytocin- and PGF₂ₐ-induced myometrial activity. Myoelectrical activity in the oviduct following treatments with oxytocin, PGF₂ₐ, and PGE₂ was characterized by an increased duration of activity bursts, intensity, and amplitude. Oxytocin and PGF₂ₐ caused a decline in the number of oviductal activity bursts, while PGE₂ treatment resulted in an increased number of activity bursts. Oxytocin treatment during diestrus resulted in longer duration of bursts compared to PGE₂ treatment, and a higher intensity compared to PGF₂ₐ and PGE₂ treatment. It was concluded that oxytocin, PGF₂ₐ, and PGE₂ affect both the myometrium and the myosalpinx in the mare.

INTRODUCTION

Electrical changes that occur in the membrane potential of the myometrium and myosalpinx can be monitored by the use of electromyography (EMG). Myoelectrical activity of the uterus has been described in the mare during late pregnancy and parturition as well as during the estrus cycle [Taverne et al., 1979; Haluska et al., 1987; Jones et al., 1991; Troedsson et al., 1993a]. Myometrial electrical activity varies with the stage of the estrus cycle in the mare [Taverne et al., 1979; Troedsson et al., 1993a] and in the cow [Ruckebusch & Bayard, 1975]. However, there are no reports on electrical activity of the myosalpinx in the mare during any phase of the estrous cycle.

Prostaglandin (PG) E₂ has been suggested to be responsible for oviductal transport of fertilized ova through stimulation of oviductal muscle activity, but the direct effect of PGE₂ or PGF₂ₐ on the oviduct has not been documented in the mare. Oxytocin, cloprostenol, and fluprostenol have been shown to affect myometrial electrical activity in the mare during both estrus and diestrus [Taverne et al., 1979; Jones et al., 1991]. Using radiotelemetry, Cross et al. [1991] observed an increase in myoelectrical activity of the uterus following the administration of PGF₂ₐ, but the duration of this activity was not clear from the study. Increased activity of the myosalpinx was observed after treatment of cows with oxytocin [Ruckebusch & Bayard, 1975], but there are no reports on electrical activity of the myosalpinx in response to PGF₂ₐ or PGE₂.

Treatment of mares with oxytocin and PGF₂ₐ after breeding has been suggested to be effective in evacuating accumulated intraluminal fluid from the uterus and potentially enhanc-
ing fertility in mares that are susceptible to chronic uterine infection [Troedsson et al., 1992; LeBlanc, 1994]. With this development in the management of susceptible mares, it is essential to understand the effect of these drugs on the myometrium. It is equally important to clarify the effect of these drugs on the oviduct, where transport and interaction of gametes take place shortly after mating.

The objectives of this study were to document normal oviductal activity during the estrous cycle by means of EMG, and to investigate the effects of oxytocin, PGF2α, and PGE2 on myoelectrical activity of the myometrium and myosalpinx in the mare.

MATERIALS AND METHODS

Mares
Five normally cycling mares with a sound reproductive history were used in this study. The mares were fed alfalfa hay and were kept in stalls. During the recordings, the mares were confined to an examination stock. The stage of the estrous cycle was determined by transrectal ultrasonographic examination (5 MHz linear array) of the reproductive tract for the detection of ovarian follicles and the presence of a CL. Estrus and diestrus was confirmed by determining concentrations of progesterone in blood samples obtained at each recording session.

Collection of Blood Samples
In conjunction with each recording session, 10 ml of venous blood was withdrawn from the jugular vein by use of a vacutainer system (Becton Dickinson, Rutherford, NJ) containing sodium heparin. The samples were centrifuged at 400 × g for 10 min, and plasma was removed and stored at −20°C until analyzed for progesterone.

Hormone Analysis
Plasma progesterone concentrations were analyzed by a solid-phase microtiter plate enzyme-immunoassay as described by Munro & Stabenfeldt [1984]. Progesterone 3-O-carboxymethylxime-horseradish peroxidase was used as the label, and antiseraum from rabbits was raised against a progesterone 11α-hemisuccinyl-bovine serum albumin (11α-hemisuccinyl-BSA) immunogen. Progesterone 3-O-carboxymethylxime and 11α-hemisuccinate-BSA were purchased from Steraloids, Inc. (Wilton, NH). Horseradish peroxidase was obtained from Sigma Chemical Co. (St. Louis, MO). The mean intraassay coefficient of variation was 9.97% and the average interassay coefficient of variation for pools of high, medium, and low progesterone concentration were 4.9, 6.2, and 10.5%, respectively. The sensitivity of the progesterone assay was < 0.1 ng ml⁻¹.

Electrode Implantation
One pair of electrodes was surgically implanted in the myosalpinx, and four pairs of electrodes were implanted in the myometrium of each mare as previously described [Troedsson et al., 1993a]. The reproductive tract was exposed via a midventral laparotomy performed under general anesthesia induced by 100 mg guaifenesin/kg BW (Rhone-Poulenc, Collegeville, PA) and 2 mg thiamylal/kg BW (Surital; Parke-Davis, Morris Plains, NJ) i.v. and maintained with halothane (Halocarbon Laboratories, N. Augusta, SC). One pair of electrodes (44-gauge multistrand stainless steel) was implanted in the myosalpinx at the site of the isthmus of the left oviduct. Four pairs of electrodes were implanted in the uterus. Three of these were implanted in the myometrium of the left uterine horn, which was spread 3–5 cm apart, one each at the tip, in the middle, and at the base of the horn. The fourth electrode was implanted in uterine body. Within each pair, the electrodes were spaced approximately 1 cm apart, arranged longitudinally in the oviduct and paralleled in the myometrium. The implantation technique allowed exposure of the electrodes to both the longitudinal and circular muscle layers. The recorded activity therefore represented the combined activity of the two muscle layers in both the myosalpinx and myometrium. Each electrode, covered by a teflon tube, was passed through the abdominal wall of the left flank, tunneled subcutaneously, exteriorized near the withers, fixed in place, and capped.

EMG Recordings
After electrode implantation and recovery from surgery, the mares were rested for one week to allow the oviduct and uterus to stabilize after surgery. Electrical activity was monitored with each electrode joined to the appropriate lead of a Grass polygraph. EMG signals were amplified through Grass DC preamplifiers, and the signals were transcribed to a Grass polygraph at a chart speed of 10 mm/min and at an amplitude of 50 μV/cm for the myos-
alpinx and 100 μV/cm for the myometrium. High and low pass signal filters were set at 10 and 35 Hz [Haluska et al., 1987].

Spontaneous oviductal electrical activity was monitored in each mare for 3 h during estrus and 4 h during diestrus. Myometrial and oviductal electrical activity in response to intravenous administration of 20 units of oxytocin (The Butler Company, Columbus, OH) and intramuscular administration of 10 mg PGF2α (Lutalyse; Upjohn, Kalamazoo, MI) was recorded during estrus and diestrus within the same estrous cycle of each mare, with 2–14 days elapsed between the recordings. Response to an i.m. injection of 10 mg PGE2 (kindly supplied by Upjohn) was recorded during diestrus 1–3 cycles later. The dose of 10 mg PGE2 was based on a preliminary dose dependence study (Troedsson, unpublished data) and was used for the purpose of comparison with PGF2α. Due to technical problems with electrodes in some mares, a complete study of the effect of PGE2 on the myometrium and myosalpinx was assessed only during diestrus. All treatments were preceded by 1–3 h of baseline recordings and then 30 min of recordings after the administration of an isotonic saline solution. Recordings of oviduct and myometrial activity continued until visual stabilization of the activity occurred.

All handling, treatments, and procedures were conducted in accordance with the NIH guide for the care and use of laboratory animals and were approved by the Animal Care and Use Committee at the University of California, Davis.

Analysis

All recordings were manually transformed to a digitized form, and myoelectrical activity was analyzed as previously described by Troedsson et al. [1993a]. The total electrical activity of the myosalpinx and myometrium was expressed as the percentage of time any activity was recorded (Fig. 1). Characteristics of myoelectrical activity were analyzed for its frequency, duration, intensity and amplitude of activity bursts (Fig. 2). An activity burst was defined as electrical activity consisting of at least 10 recorded spikes/min and separated from other bursts by at least 1 min. Frequency was defined as the number of activity burst per 30 min. Duration was defined as the time (in minutes) that elapsed from the start to the end of a burst. Intensity was defined as the number of spikes within an activity burst per minute. Intensity was coded as low = I (10–15 spikes/min), intermediate = II (16–20 spikes/min), or high = III (> 20 spikes/min). Amplitude was defined as the highest recorded amplitude of spikes in a burst for each minute. Amplitude was coded as low (< 50 μV), intermediate (50–100 μV), or high (> 100 μV). The amplitude of EMG registrations depends upon the number of active muscle cells in the range of the recording electrodes, and a complete standardization of the distances of the impedances of electrodes in the myometrium and the myosalpinx was not possible. Comparisons of the amplitude of electrical activity during estrus and diestrus, and between different treatments, were possible in this study since alterations of EMG in relation to treatments and stages of the estrous cycle were compared within mares and within each pair of electrodes. Amplitude of activity bursts in the myosalpinx and in the myometrium was not compared.

Statistical Analysis

Myometrial electrical activity was calculated as the average activity recorded from each pair of electrodes in the myometrium. The differences in each response variable between the average of the replicates of the pretreatment period and of the treatment period were analyzed by means of a split-plot analysis of variance (ANOVA), with the mare used as a blocking variable. The treatments were oxytocin, PGF2α, PGE2, and saline. The whole-plot portion of the analyses was the location in the mare where the measurements were taken: the oviduct or myometrium. The subplot portion was a combination of the treatments and the phase of the estrous cycle during which the measurements were taken: estrus or diestrus. Treatment and stage of the estrous cycle were combined into one independent variable because the PGE2 treatment was applied only in the diestrus portion of the cycle. All comparisons of interest including interaction between treatments and stage of cycle were performed by use of contrasts and the proper error term. Results were expressed as means ± SEM. Significance was claimed when p < 0.05.

RESULTS

Mean concentrations of progesterone in plasma of mares recorded during estrus were
FIG. 1. Ninety minutes of recordings of myoelectrical activity in the oviduct (A), and the myometrium (B-E) in response to 20 IU of oxytocin administered during diestrus. The arrow indicates administration of oxytocin. Electrodes were implanted in the oviduct (A); the tip (B), the middle (C), and the base (D) of the left uterine horn; and the uterine body (E). Both the myosalpinx and the myometrium responded with one hour of increased total electrical activity.
FIG. 2.  
a) Example of activity bursts with different intensities. Intensity was defined as the number of spikes per minute. Intensity was coded as low (I, 10-15 spikes/min), medium (II, 16-20 spikes/min), and high (III, > 20 spikes/min). b) Thirty minutes of recordings of myometrial electrical activity from the tip of the left uterine horn between 30 and 60 minutes following the administration of 10 mg PGF₂α. The activity bursts have a high intensity, 2-3 minutes duration, and a frequency of 6 bursts per 30 minutes. c) Thirty minutes of recordings of oviductal electrical activity 4 hours after administration of PGF₂α. Example of low (< 50 µV), medium (50-100 µV), and high (> 100 µV) amplitude.
activity bursts were similar in recordings made during estrus and diestrus (Table 1). Significantly more activity was observed in the myosalpinx than in the myometrium throughout the estrous cycle (59.3 ± 2.7% vs. 28.8 ± 1.6%; \( p < 0.01 \)). Similar differences between the myosalpinx and the myometrium were seen after treatments with oxytocin and PGF\(_{2\alpha}\) during estrus as well as during diestrus \( (p < 0.0001) \). Characteristics of the electrical activity in the myosalpinx differed from those in the myometrium. Significantly more activity bursts per time unit were registered in the myosalpinx than in the myometrium \( (3.1 ± 0.16/30 \text{ min} vs. 2.5 ± 0.18/30 \text{ min}; p < 0.05) \). In addition, the durations of activity bursts in the myosalpinx were longer than in the myometrium \( (6.2 ± 0.76 \text{ min} vs. 3.4 ± 0.36 \text{ min}; p < 0.01) \). No significant differences in the intensity of electrical activity were found between the myosalpinx and the myometrium.

**Oxytocin**

Intravenous administration of 20 IU of oxytocin during estrus resulted in an increased myometrial activity for 1 h \( (p < 0.0001) \) (Fig. 3). The increased activity was characterized by an increase in the number of activity bursts \( (p < 0.005) \), but the duration of activity bursts was not consistently affected by oxytocin \( (p < 0.08; \text{Fig. 4}) \). Both the intensity \( (p < 0.005) \) and the amplitude \( (p < 0.01) \) of electrical activity in the myometrium were significantly increased after treatment.

As in the treatment response during estrus, oxytocin treatment during diestrus resulted in increased myometrial electrical activity that lasted for 1 h \( (p < 0.0001; \text{Fig. 5}) \). The frequency of activity bursts was not significantly altered by the treatment, but the bursts were characterized by increased durations \( (p < 0.0001) \), increased intensity \( (p < 0.0005) \), and an elevation of the amplitude \( (p < 0.01; \text{Fig. 6}) \).

Although oxytocin-induced total activity in the myometrium was similar during estrus and diestrus during estrus, the frequency, intensity, and amplitude of electrical activity bursts were significantly different. The intensity of electrical activity was highest during estrus, and the amplitude was highest during diestrus. The duration of activity bursts was not significantly affected by oxytocin treatment during estrus or diestrus.

**Table 1.** Spontaneous myoelectrical activity of the oviduct during estrus and diestrus (all values are mean ± SEM).

<table>
<thead>
<tr>
<th>Stage of cycle</th>
<th>Frequency (burst 30 min(^{-1}))</th>
<th>Duration (min)</th>
<th>Intensity (1-3) (^{a})</th>
<th>Total activity (%)</th>
<th>Amplitude (1-3) (^{b})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estrus</td>
<td>3.0 ± 0.14</td>
<td>5.9 ± 0.56</td>
<td>2.0 ± 0.06</td>
<td>58.3 ± 3.14</td>
<td>1.9 ± 0.10</td>
</tr>
<tr>
<td>Diestrus</td>
<td>3.2 ± 0.18</td>
<td>6.4 ± 0.99</td>
<td>1.7 ± 0.07</td>
<td>60.0 ± 4.50</td>
<td>1.7 ± 0.10</td>
</tr>
</tbody>
</table>

\(^{a}\) 1, low (10-15 spikes min\(^{-1}\)); 2, intermediate (16-20 spikes min\(^{-1}\)); 3, high (> 20 spikes min\(^{-1}\)).

\(^{b}\) 1, low (< 50 μV); 2, intermediate (50-100 μV); 3, high (> 100 μV).
and diestrus, an increase in the number of activity bursts (4.1 ± 0.52 vs. 1.8 ± 0.15/30 min) with shorter durations (6.4 ± 1.60 vs. 14.1 ± 2.30/min) was observed after oxytocin treatment in estrus compared to diestrus (p < 0.005).

Electrical activity in the myosalpinx during estrus was significantly increased for 1 h after intravenous administration of 20 IU oxytocin (p < 0.001; Fig. 3). The oviductal activity was characterized by a decline in the number of activity bursts (p < 0.01) and significant increase in the duration of activity bursts (p < 0.0001; Fig. 7). A significant increase in the intensity of oviductal electrical activity (p < 0.004) and a tendency to increased amplitude was also found (p = 0.05).

The myosalpinx was also affected by oxytocin treatment during diestrus (Fig. 5). A significant increase in electrical activity of the myosalpinx was observed for 1 h after the administration of oxytocin (p < 0.0001). The characteristics of the increased activity during diestrus resembled the response during estrus, with fewer activity bursts (p < 0.0001) of increased duration (p < 0.0001) and intensity (p < 0.0001) during the affected period (Fig. 8). The increased duration of activity bursts as a response to oxytocin treatment was more marked when mares were treated during diestrus compared to estrus (27.3 ± 2.28 vs. 20.6 ± 3.13 min; p < 0.01). The amplitude of the electrical activity was not affected by oxytocin treatment during diestrus.
FIG. 5. Total myoelectrical activity of oviduct (a) and myometrium (b) in response to 20 IU oxytocin (closed squares), 10 mg PGF$_2$α (closed diamonds), and 10 mg PGE$_2$ (closed triangles) during diestrus. NaCl indicates time when saline was administered. Treatments (Tx) were administered immediately after Time 0. Duration of treatment effect in oviduct and myometrium was 4.5 h for PGF$_2$α, 2 h for PGE$_2$, and 1 h for oxytocin.

PGF$_2$α

Intramuscular injection of 10 mg PGF$_2$α during estrus resulted in a significant increase of myometrial activity for 5 h ($p < 0.002$) (Fig. 3). The PGF$_2$α-induced electrical activity was characterized by an elevated number of activity bursts ($p < 0.0001$) of increased intensity ($p < 0.0001$) and amplitude ($p < 0.005$) (Fig. 4). No persistent alterations of the duration of activity bursts were observed.

A significant myometrial response that lasted for 4.5 h was found when mares were treated with PGF$_2$α during diestrus ($p < 0.001$) (Fig. 5). The increased electrical activity was characterized by an elevated number of activity bursts ($p < 0.05$) with increased duration ($p < 0.001$) and intensity ($p < 0.01$; Fig. 6). The amplitude of the electrical myometrial activity was not affected by PGF$_2$α treatment during diestrus.

Mean total myometrial activity in response to PGF$_2$α did not differ between mares that were treated during estrus and those treated during diestrus. However, more frequent activity bursts were found when mares were treated in estrus compared to diestrus (3.3 ± 0.16 vs. 5.2 ± 0.35/min; $p < 0.05$). The activity bursts tended to be of shorter duration in mares treated during estrus than in mares treated during diestrus (4.8 ± 0.49 vs. 9.3 ± 0.89 min; $p < 0.06$). Furthermore, the activity bursts had a higher amplitude when mares were treated in estrus compared to mares treated during diestrus (2.6 ± 0.05 vs. 2.0 ± 0.07; $p < 0.02$).

Mares treated with PGF$_2$α during estrus responded with increased electrical activity in the myosalpinx for 5 h ($p < 0.01$; Fig. 3). The increased activity was characterized by a significant decline in the number of activity bursts ($p < 0.05$), which had an increased duration ($p < 0.0001$), increased intensity ($p < 0.005$), and elevated amplitude ($p < 0.005$; Fig. 7).

Mares treated with PGF$_2$α during diestrus responded with significantly elevated oviducal activity for 4.5 h ($p < 0.005$; Fig. 5). Increased durations of activity bursts ($p < 0.0001$) and increased intensity ($p < 0.05$) were the only consistent alterations in the pattern of electrical activity (Fig. 8). Neither the mean total oviductal activity nor its characteristics following treatment with PGF$_2$α were affected by the stage of the estrous cycle.

PGE$_2$

Myometrial and oviducal response to PGE$_2$ was investigated only during diestrus. The myometrium responded with increased myometrial activity for 2 h after the administration of 10 mg PGE$_2$ ($p < 0.01$; Fig. 5). The duration of myometrial activity bursts increased significantly after treatment ($p < 0.005$), and the bursts were characterized by an increase in both intensity ($p < 0.005$) and amplitude ($p < 0.05$; Fig. 6).

PGE$_2$ treatment affected the myosalpinx with increased electrical activity for more than 2 h ($p < 0.005$; Fig. 5). The increased activity was characterized by an elevated number of activity bursts ($p < 0.01$) with increased duration ($p < 0.05$; Fig. 8). The intensity and amplitude of the activity bursts were not affected by treatment.
Comparison of Treatments

The duration of the effect of PGF$_{2a}$ on oviductal and myometrial activity was longer (5 h) than that of PGE$_2$ (2 h), and oxytocin had the shortest duration (1 h) ($p < 0.0001$). For the duration of the treatments' effects, no differences between the mean total uterine or oviducal myoelectrical activity were detected resulting from treatments used in this study. The characteristics of the induced myometrial response did not differ between treatments during estrus (Fig. 4). The only observed difference in myometrial response to various treatments was found between oxytocin and PGF$_{2a}$ when mares were treated during diestrus (Fig. 6). Oxytocin resulted in significantly fewer activity bursts compared to PGF$_{2a}$ ($p < 0.01$).

The characteristics of treatment-induced electrical activity in the myosalpinx were not different for oxytocin and PGF$_{2a}$ when the mares were treated during estrus (Fig. 7). However, the myosalpinx responded differently to the treatments during diestrus (Fig. 8). The number of activity bursts in the myosalpinx declined after treatment with oxytocin and did not change after treatment with PGE$_2$. In contrast, PGE$_2$ treatment resulted in increased frequency of activity bursts that was statistically different from the effect of oxytocin ($p < 0.0001$) and PGF$_{2a}$ ($p < 0.003$). The intensity of activity bursts during diestrus was higher after treatment with oxytocin during diestrus than after treatments during the same time with PGF$_{2a}$ ($p < 0.05$) and PGE$_2$ ($p$
FIG. 7. Number of activity bursts per 30 min (a), duration of activity bursts (b), and intensity (c) and amplitude (d) of myoelectrical activity of oviduct in response to 10 IU oxytocin (closed squares) and 10 mg PGF$_{2a}$ (closed diamonds) during estrus. NaCl indicates time when saline was administered. Treatments (Tx) were administered immediately after Time 0. Induced activity was characterized by decline in frequency (oxytocin: $p < 0.01$; PGF$_{2a}$: $p < 0.05$), but increased duration of activity bursts (oxytocin: $p < 0.0001$; PGF$_{2a}$: $p < 0.0001$), increased intensity (oxytocin: $p < 0.004$; PGF$_{2a}$: $p < 0.005$) and increased amplitude (oxytocin: $p = 0.05$; PGF$_{2a}$: $p < 0.005$).

DISCUSSION

EMG measures changes in action potentials over the membrane of the muscle cell in the range of the recording electrodes. A close relationship between electrical and mechanical activity has been demonstrated in the myometrium [Toutaine et al., 1983]. Furthermore, EMG analyses of the myometrium have been shown to give more consistent results and to be a more accurate method for measuring uterine motility compared to intrauterine pressure recordings [Jones et al., 1991]. In the present study, the term electrical activity, rather than uterine or oviductal contractions, was used to describe the recorded EMG activity.

This is the first report on myoelectrical activity in the oviduct in the mare. Electrical activity in the myosalpinx was not altered by the estrous cycle under conditions of this study. Previous reports on myometrial activity in the mare demonstrated changes in electrical myometrial activity between different stages of the estrous cycle [Taverne et al., 1979; Jones et al., 1991; Troedsson et al., 1993a]. Oviductal activity has been shown to be affected by the estrous cycle in other species. With use of EMG, it was found that electrical activity of the myosalpinx in the cow increases during estrus compared to diestrus [Ruckebusch & Bayard, 1975]. Intraluminal pressure microtransducers were used to measure oviductal activity in cows and pigs [Rodriguez-Martinez et al., 1982; Bennet et al., 1983].
MYOELECTRICAL ACTIVITY IN THE MYOSALPINX AND MYOMETRIUM

FIG. 8. Number of activity bursts per 30 min (a), duration of activity bursts (b), and intensity (c) and amplitude (d) of myoelectrical activity of oviduct in response to 10 IU oxytocin (closed squares), 10 mg PGF\textsubscript{2\alpha} (closed diamonds) and 10 mg PGE\textsubscript{2} (closed triangles) during diestrus. NaCl indicates time when saline was administered. Treatments (Tx) were administered immediately after Time 0. Frequency of activity bursts decreased after treatment with oxytocin (p < 0.0001) but increased after treatment with PGE\textsubscript{2} (p < 0.01). Duration of activity bursts increased after treatment with oxytocin (p < 0.0001), PGF\textsubscript{2\alpha} (p < 0.0001), and PGE\textsubscript{2} (p < 0.05). Intensity of activity increased after treatment with oxytocin (p < 0.0001) and PGF\textsubscript{2\alpha} (p < 0.05). Amplitude was not affected by any of the treatments.

1988; Pettersson, 1991]. These studies also found an increase in oviductal activity in animals during estrus compared to diestrus. Intraluminal pressure transducers monitor oviductal activity by responding to increases and decreases in the internal diameter of the oviduct. Contraction of the circular muscle layers of the oviduct produce a decrease in the diameter of the transducer, while contractions in the longitudinal muscle layers produce a shortening of the oviduct and a corresponding increase in the transducer diameter [Blair & Beck, 1977]. In vivo monitoring of EMG activity of the myosalpinx does not allow for separate registration of the two muscle layers but rather registers the combined oviductal muscle activity. Further studies that compare intraoviductal microtransducers with EMG are needed to validate the finding of no effect of estrous cycle on oviductal activity in the mare in comparison to findings in other species.

More electrical activity was consistently found in the myosalpinx than in the myometrium during all treatments and stages of the estrous cycle. This higher activity was the result of an increased number and longer duration of activity bursts in the myosalpinx, without any difference in the intensity of electrical activity. Similar differences in electrical activity between the myosalpinx and the myometrium have been reported in cows during estrus [Ruckebusch & Bayard, 1975].

It is well known that estrogen in many species increases the concentration of oxytocin receptors and their affinity in myometrial sarcolemma, whereas progesterone is believed to
have the opposite effect [Roberts et al., 1976; Fuchs et al., 1983; Soloff et al., 1983]. Oxytocin binding sites in the mare have been reported to fluctuate throughout the estrous cycle, with highest concentrations at the time of luteolysis [Stull & Evans, 1986]. The results from this study suggest that the equine myometrium and myosalpinx have sufficient receptor concentrations to respond to a pharmacological dose of oxytocin during both estrus and diestrus. This supports the findings by Goddard & Allen (1985) and Ko et al. (1989). Jones et al. (1991) also observed that mares responded to oxytocin in all cycle stages, but they found a less pronounced response during diestrus. In the present study, oxytocin’s effect on the myometrium was similar during estrus and diestrus with respect to the duration of the entire response, the total activity, and the intensity and amplitude of activity bursts. However, an increased number of activity bursts with shorter duration was observed when mares were treated in estrus compared to diestrus. These changes in the pattern of electrical activity in the myometrium are in agreement with previous findings on spontaneous myoelectrical activity during the estrous cycle [Troedsson et al., 1993a]. The different characteristics of myoelectrical activity in the myometrium between estrus and diestrus were proposed in that study to be the result of hormone-dependent changes in myometrial cell communication such as the formation of gap junctions.

Exogenous PGF2α resulted in increased myometrial and oviducal activity for 4.5–5.0 h after treatment. This effect is significantly longer than previously reported. Goddard & Allen (1985) reported increased myometrial activity following the administration of PGF2α for 60 min, but the dose used was four times less than in this study. The stage of the estrous cycle at the time of treatment with PGF2α influenced the duration of the effect but not the mean total activity. These observations combined with findings of more frequent activity bursts with shorter duration and higher amplitude in mares treated during estrus correlate well with those expected in a uterus that is exposed to estrogen without the presence of progesterone [Troedsson et al., 1993a].

This is the first report on the effect of PGE2 on myometrial activity in the mare. The equine embryo has been shown to secrete PGE2 [Watson & Sertich, 1989; Weber et al., 1991a; Weber et al., 1992]. Embryo-secreted PGE2 is suggested to cause myometrial contractions responsible for the migration of the embryo within the uterus for the first 16 days of pregnancy [Vanderwall et al., 1993]. However, the authors did not demonstrate this role of PGE2. In the present study, the administration of 10 mg PGE2 resulted in increased myometrial electrical activity for 2 h. The increased activity was characterized by increased intensity and amplitude, suggesting a potential role for PGE2 in embryonic migration in the uterus.

The myosalpinx responded with increased electrical activity after all treatments. Studies in rabbits and pigs have shown a stimulatory effect of PGF2α on the longitudinal muscle layer, resulting in an increased internal oviducal diameter [Blair & Beck, 1977; Rodriguez-Martinez & Einarsson, 1985]. In contrast, PGE2 blocked spontaneous activity of longitudinal and circular muscle layers but caused little change in the oviducal diameter [Blair & Beck, 1977]. In the pig, the effect of PGE2 on the oviduct is dependent on the stage of the cycle, being inhibitory of the circular layer but stimulatory of the longitudinal layer during estrus and stimulatory of both layers during diestrus [Rodriguez-Martinez & Einarsson, 1985]. However, in the pig and the rabbit, a stimulatory effect of PGF2α and not the inhibitory effect of PGE2 is believed to be the most important mechanism for egg transport through the oviduct [Aref et al., 1973; Chang et al., 1973; Blair & Beck, 1977; Rodriguez-Martinez & Einarsson, 1985]. In the mare, on the other hand, PGE2 is considered to be more important than PGF2α for selective oviductal transport of the fertilized egg [Weber et al., 1991b]. This study demonstrated an effect on the myosalpinx of both PGF2α and PGE2. The effect of PGF2α and oxytocin on the longitudinal and circular muscle layers of the myosalpinx in the mare must be clarified for full understanding of how these hormones may affect gamete transport and interaction in the oviduct.

Impaired uterine clearance has been shown to be a major cause of persistent endometritis in the mare, and the use of exogenous oxytocin and PGE2 have both been reported to be effective in evacuating accumulated intraluminal uterine fluids and inflammatory products in mares with persistent endometritis [Troedsson (AUS: & Liu, 1991; Troedsson et al., 1992, 1993b; Le Blanc, 1994). When these drugs are used after breeding, the adverse effect on sperm and ovum transport in the oviduct and on the embryo’s descent to the uterus should
be considered. The prolonged duration of the effect of PGF$_{2a}$ compared to oxytocin on both myometrial and oviductal activity should be considered before these hormones are used as postbreeding treatments.

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