Episodic secretion of gonadotrophins and ovarian steroids in jugular and utero-ovarian vein plasma during the follicular phase of the oestrous cycle in gilts*

B. Flowers†, T. C. Cantley, M. J. Martin and B. N. Day

Department of Animal Science, University of Missouri, Columbia, MO 65211, USA

Summary. Blood samples were collected simultaneously from the jugular and utero-ovarian veins of 13 gilts from Days 11 through 16 of the oestrous cycle. A luteolytic dose (10 mg) of PGF-2α was given on Day 12 to facilitate the natural occurrence of luteolysis and standardize the associated decrease in concentrations of progesterone. The mean interval from PGF to oestrus was 5.5 ± 0.7 days (mean oestrous cycle length = 17.5 ± 0.7 days). Mean concentrations, pulse amplitudes and pulse frequencies of oestradiol and progesterone were greater (P < 0.05) in the utero-ovarian than jugular vein. Secretory profiles of LH and FSH were similar (P > 0.05) in plasma collected simultaneously from both veins. Based on these data, temporal relationships among hormonal patterns of FSH and LH in the jugular vein and oestradiol and progesterone in the utero-ovarian vein were examined. Concentrations of progesterone declined (P < 0.05) between Days 12 and 14, while all secretory variables for oestradiol increased (P < 0.05) from Day 12 through 16 of the oestrous cycle. The pulsatile secretion of FSH remained relatively constant during the experiment. However, both pulse amplitude and mean concentration tended (P < 0.2) to be lower on Day 16 compared with Day 12. The episodic secretion of LH shifted from a pattern characterized by high-amplitude, low-frequency pulses to one dominated by numerous pulses of diminishing magnitude between Days 13 and 14. From Days 14 to 16 of the oestrous cycle, 91% of all oestradiol pulses were temporally associated with gonadotrophin pulses composed of both FSH and LH episodes. However, pulses of oestradiol (52%) not associated with an episode of LH and/or FSH were observed on Days 12 and 13. These data demonstrate that during the follicular phase of the pig oestrous cycle substantial oestradiol production occurred coincident with luteolysis and before the shift in the episodic secretion of LH. The pool of follicles which ovulated was probably the source of this early increase in the secretion of oestradiol. Therefore, we propose that factors in addition to FSH and LH are involved in the initial selection of follicles destined to ovulate during the early stages of the follicular phase of the pig oestrous cycle. In contrast, high-frequency, low-amplitude pulses composed of LH and FSH were the predominant endocrine signal associated with oestradiol secretion during the second half of the oestrous cycle. We therefore suggest that alterations in gonadotrophic stimuli account for the majority of follicular growth and steroidogenesis during the final stages of development before ovulation.

Keywords: hormonal episodes; gonadotrophins; ovarian steroids; follicular growth; gilts

*Reprint requests to Dr B. N. Day.
†Present address: Department of Animal Science, North Carolina State University, Raleigh, NC 27695-7621, USA.
Introduction

Changes in the secretion of gonadotrophins and ovarian steroids during the follicular phase of the pig oestrous cycle have been described previously (Henricks et al., 1972; Aherne et al., 1976; Parviz et al., 1976; Van de Wiel et al., 1981). In general, after Day 12, progesterone concentrations decrease, while concentrations of oestradiol-17β increase. The episodic secretion of luteinizing hormone (LH) shifts from a pattern predominated by low-frequency, high-amplitude pulses to one characterized by numerous pulses of diminishing size (Kopf et al., 1983). Follicle-stimulating hormone (FSH) is also secreted in a pulsatile fashion, but the frequency and amplitude of FSH episodes appear to remain relatively constant between luteolysis and oestrus. Despite this information, several important questions concerning the functional and temporal relationships among these hormonal events remain unanswered for pigs (Foxcroft & Van de Wiel, 1982). These include: (1) does the pattern of gonadotrophin secretion from the pituitary gland arrive unaltered at the ovary; (2) does the ovary respond to pulses of gonadotrophins with an episodic release of steroid hormones; and, perhaps most importantly, (3) after the decline in progesterone which event occurs first—the increase in oestradiol or the shift in the pulsatile secretion of LH?

In order to answer these questions, an evaluation of hormonal changes at the level of both the pituitary gland and the ovary is required. In pigs, the jugular vein receives the venous drainage from the vessels leaving the pituitary gland, while ovarian hormones enter the peripheral circulation via the ovarian branch of the utero-ovarian vein (Oxenreider et al., 1965). Consequently, from an anatomical stand-point, hormonal patterns in the jugular and utero-ovarian veins should represent a precise and accurate estimation of the secretory activity of the pituitary gland and ovary, respectively. Previous studies, upon which most of the current information with regard to the endocrinology of the oestrous cycle is based, have not evaluated simultaneously hormonal profiles of gonadal steroids and gonadotrophins in the utero-ovarian vein during periods of active follicular development in pigs.

Therefore, the objective of the present study was to characterize the secretory profiles of LH, FSH, oestradiol-17β and progesterone in the jugular and utero-ovarian vein during the follicular phase of the pig oestrous cycle. Apart from further defining temporal and cause and effect relationships among these hormones, the underlying purpose of this study was to provide further insight into the endocrine regulation of follicular development during the oestrous cycle.

Materials and Methods

Experimental animals. Sixteen mature crossbred gilts (Yorkshire-Duroc-Landrace, 9–10 months of age, 127–130 kg) were used in the study. All gilts exhibited 3 oestrous cycles of normal length (19.1 ± 9.9 days) and normal oestrous behaviour before the onset of the experiment. Females were housed in an environmentally controlled building during the study. They were fed a complete corn-soybean meal maintenance diet twice daily and had access to water ad libitum.

Experimental procedure. On Day 8 of the oestrous cycle (Day 0 = first day of oestrus), tygon catheters (0.63 mm i.d. × 1.07 mm o.d.; Storz Instrument Co., St Louis, MO, USA) were placed in a utero-ovarian and jugular vein of each gilt. For all catherizations, anaesthesia was induced with sodium thiopental (1 g) and maintained with a closed-circuit system of halothane, nitrous oxide and oxygen. Jugular catheters were inserted according to the procedure of Ford & Maurer (1978). The end of each jugular catheter was 6 cm cranial to the junction of the jugular vein and cranial venous cava. Catheterization of the utero-ovarian vein was performed in the following manner. One horn of the uterus was exposed through a midventral incision. At 20–25 cm from the tip of the uterine horn, a 2-cm portion of a branch of the utero-ovarian vein (Oxenreider et al., 1965) was exposed via a parallel cut in the mesometrium. The catheter was inserted maximally 35 cm (depending on the size of the uterus) so that the tip lay 1 cm cranial to the entrance of the ovarian branch of the utero-ovarian vein. Mesometrium was then drawn around and over the catheter and the partly severed vein by a "purse-string" suture. Movement of the catheter within the vein was prevented by at least 3 tie-down stitches (3–5 cm apart) that secured the catheter to the mesometrium. The catheter was exteriorized via a puncture wound in the paralumbar fossa using a trochar and cannula. At the end of the experiment, catheters
were removed surgically and their location within the utero-ovarian vein was verified. Data from 3 animals were excluded due to dislocation of the utero-ovarian vein catheter.

Blood samples were collected simultaneously every 15 min for 6 h (08:00–14:00 h) from the jugular (4 ml) and utero-ovarian (3 ml) veins from Day 11 through oestrus. On Day 12 of the oestrous cycle, a luteolytic dose (10 mg i.m.) of prostaglandin F-2α (Lutalyse; The UpJohn Co., Kalamazoo, MI, USA) was given before the beginning of the sampling period. This was done to facilitate the natural occurrence of luteolysis and standardize the associated decrease in progesterone (Hallford et al., 1975; Guthrie & Polge, 1976). Samples were collected in heparinized syringes and stored on ice. At the end of each 6-h collection period, plasma was separated from cellular components by refrigerated centrifugation (1200 g, 4°C, 15 min) and stored at −20°C. Occurrence of oestrus was checked with a mature boar each day at 3 h after the completion of the sampling period. The mean interval from PGF to oestrus was 5.5 ± 0.7 days (mean oestrous cycle length = 17.5 ± 0.7 days).

**Hormone analysis.** A double-antibody radioimmunoassay described by Niswender et al. (1970) was used to determine plasma concentrations of LH. Anti-porcine LH (â55) was used as the first antibody. Purified pig LH (LER-783-3) served as the labelled tracer and standard. Inter- and intra-assay coefficients of variation were 13.5 and 11.7%, respectively. Assay sensitivity, defined as 90% of total binding, was 0.2 ng/ml.

Plasma concentrations of FSH were determined by a double-antibody radioimmunoassay described by Redmer et al. (1984). Anti-porcine FSH (1533) that was specific against the pig FSH β-subunit was used as the first antibody (Bio-Products, UCB, Brussels, Belgium). Purified pig FSH (pFSH IA3-c2, 26-1 units/mg NIH-FSH-S1) was used as the labelled tracer and standard. Inter- and intra-assay coefficients of variation and assay sensitivity were 12.4%, 10.4% and 0.4 ng/ml, respectively.

A radioimmunoassay described by Kessler et al. (1977) and validated for pigs by Redmer & Day (1981) was used to determine plasma concentrations of oestradiol-17β. Inter- and intra-assay coefficients of variation were 12.8 and 9.7%, respectively. Mean recovery rate of [2,4,6,7-3H]oestradiol-17β from the extraction process was 89.3 ± 4.1%. Assay sensitivity was 4.1 pg/ml.

Progesterone concentrations were measured by radioimmunoassay procedures described by Flowers et al. (1989). Mean inter- and intra-assay coefficients of variation were 9.7 and 6.5%, respectively. Assay sensitivity was 0.2 ng/ml.

**Statistical analysis.** All analyses were conducted using General Linear Models procedures of the Statistical Analysis System (SAS, 1982). A split-plot analysis of variance for repeated measures (Gill & Hafs, 1971) was used to determine acute changes in the utero-ovarian vein concentrations of oestradiol after the administration of PGF. The main plot was treatment (before PGF, Day 11 vs after PGF, Day 12) and the sub-plot was time (0 to 6 h) within treatment. The animal within treatment mean square was used to test the main effect of treatment.

Mean daily concentrations of LH, FSH, oestradiol and progesterone were analysed using a split-plot-in-time analysis of variance (Gill & Hafs, 1971). The statistical model included site of sampling (site), day of the oestrous cycle, gilt, gilt within site and the site × day and gilt within site × day interactions. The main effect of site of sampling was tested using the gilt within site mean square as the error term. When a significant interaction was present (P < 0.05), modifications of this model were used to evaluate changes over days of the oestrous cycle within the jugular and utero-ovarian veins.

During each 6-h sampling period, hormonal pulses were defined according to the following criteria: (1) an increase of at least 2 standard deviations (based on the 6-h period) above the lowest preceding nadir; (2) occurrence of the peak value within 2 sampling periods of the nadir; and (3) presence of at least one point on the descending shoulder of the pulse greater than the nadir. Pulse amplitude was the peak concentration minus the nadir. The number of pulses and pulse amplitudes for LH, FSH and oestradiol were analysed using a split-plot analysis of variance (Gill & Hafs, 1971). The statistical model was identical to the model described in the previous paragraph.

Temporal relationships among pulses of LH and FSH in jugular plasma and oestradiol in utero-ovarian plasma were determined by calculating the number of pulses that occurred concomitantly or within 45 min of the start of a pulse of another hormone (Walters et al., 1984). Analysis of variance procedures for categorical data (Snedecor & Cochran, 1980; SAS, 1982) were used to analyse concomitant and associated pulse data. Treatment mean comparisons for all hormonal data were evaluated by the least significant difference test (Snedecor & Cochran, 1980).

**Results**

**FSH**

Site of sampling did not affect (P > 0.05) secretory characteristics of FSH (Fig. 1). In both blood vessels that were sampled, pulse amplitude and mean daily concentrations tended (P < 0.2) to be lower on Day-16 compared with Day-12 values.

**LH**

No differences (P > 0.05) were observed in mean concentrations, pulse frequency and pulse amplitude between plasma from the jugular and utero-ovarian veins (Fig. 2). Similarly, day of the
oestrous cycle did not influence \( (P > 0.05) \) mean concentrations of LH. In contrast, the frequency and amplitude of LH pulses increased \( (P < 0.05) \) and decreased \( (P < 0.05) \), respectively, during the experiment. Pulse frequency increased from 1.1 ± 0.2 pulses/6 h on Day 13 to 2.5 ± 0.3 pulses/6 h on Day 14. During the same time period, pulse amplitude decreased from 2.0 ± 0.2 to 0.9 ± 0.2 ng/ml.

**Oestradiol-17β**

A significant site of sampling \( \times \) day interaction \( (P < 0.05) \) was observed for secretory parameters of oestradiol-17β (Fig. 3). The frequency and amplitude of oestradiol pulses in jugular vein plasma were similar \( (P > 0.05) \) on Days 11 through 14, increased \( (P < 0.05) \) on Day 15 and remained elevated on Day 16. In contrast, a steady increase \( (P < 0.05) \) in the pulsatile secretion (frequency and amplitude) of oestradiol was observed between Days 11 and 15 of the oestrous cycle in plasma collected from the utero-ovarian vein. Alterations in the mean daily concentrations of oestradiol paralleled observed changes in its episodic release. In addition to these qualitative differences, the episodic secretion and mean concentrations of oestradiol were greater \( (P < 0.05) \) in plasma from the utero-ovarian than jugular veins during each daily sampling period.

Acute changes in oestradiol concentrations in the utero-ovarian vein before (Day 11) and after (Day 12) treatment with PGF are illustrated in Fig. 4. Analysis of variance procedures revealed a treatment by time interaction \( (P < 0.05) \). Before the administration of PGF, oestradiol-17β concentrations were not different \( (P > 0.05) \) over time during the collection period. However, on Day
Fig. 2. Mean (± s.e.m.) daily concentrations, pulse frequencies and pulse amplitudes of LH in plasma collected from the jugular and utero-ovarian (UOV) veins on Days 11 through 16 of the oestrous cycle (13 gilts). A luteolytic dose of PGF was given before sampling on Day 12.

12 (after PGF), plasma concentrations increased ($P < 0.05$) from $9.7 ± 2.1$ ng/ml at Hour 0 to $58.7 ± 7.1$ ng/ml at Hour 6.

**Progesterone**

Daily concentrations of progesterone were 3–10-times higher ($P < 0.05$) in utero-ovarian than jugular vein plasma (Fig. 5). In addition, we statistically were not able to detect pulses of progesterone in plasma from the jugular vein, while episodic secretion was evident in utero-ovarian vein plasma before Day 14 (data not shown). Consequently, statistical evaluations for pulsatile characteristics of progesterone secretion were not conducted. In both the jugular and utero-ovarian vein, a steady decline ($P < 0.05$) in progesterone concentrations occurred between Days 11 and 14 of the oestrous cycle.

**Relationship between LH and FSH pulses**

From Days 11 through 16 of the oestrous cycle, 93–100% of all LH pulses were associated with a pulse of FSH (Table 1). In contrast, the number of FSH pulses that occurred within 45 min of a
pulsed LH increased ($P < 0.05$) from 42% on Day 12 to 92% on Day 15. This temporal relationship between LH and FSH is illustrated in the individual hormonal profile of one gilt from Days 12 to 15 of the oestrous cycle (Fig. 6).

**Relationship between LH/FSH and oestradiol pulses**

No separate pulses of FSH occurred within 45 min of a pulse of oestradiol (Fig. 6). In contrast, gonadotrophin pulses consisting of both LH and FSH episodes (LH/FSH) were related temporally with pulses of oestradiol (Table 2; Fig. 6). Pulses of oestradiol that were not associated with the pulsatile secretion of gonadotrophins also were observed. On Days 12 and 13 of the oestrous cycle, 53 and 52% of oestradiol pulses occurred independent of pulses of LH/FSH. However, by Day 15, 90% of the oestradiol pulses were temporally associated with a gonadotrophic episode (Table 2).

**Discussion**

Results from studies conducted in cattle (Schallenberger et al., 1984; Walters et al., 1984) and sheep (Baird & McNeilly, 1981; Baird, 1983) indicate that the sequence of endocrine events associated
Fig. 4. Acute changes (15-min intervals over 6 h) in concentrations of oestradiol-17β in plasma from the utero-ovarian vein before and after PGF. Values represent means ± s.e.m. for 13 animals.

Fig. 5. Mean (± s.e.m.) daily concentrations of progesterone in plasma collected from the jugular and utero-ovarian (UOV) veins on Days 11 through 16 of the oestrous cycle (13 gilts). A luteolytic dose of PGF was given before sampling on Day 12.

with the selection and maturation of ovulatory follicles involves: (1) a decrease in progesterone concentrations; (2) a 2–4-fold increase in the secretion of LH; and (3) an increase in oestradiol production. Consequently, in these species, increased LH secretion associated with luteolysis is presumed to initiate the growth of follicles destined to ovulate and subsequent steroid production during the oestrous cycle.

In our study with pigs, the decline in progesterone began on Day 12 with the administration of PGF. Significant increases in the mean concentration and episodic release of oestradiol occurred on Days 12 and 13, while high-frequency, low-amplitude pulses of LH were not observed until Day 14. Collectively, these results demonstrate that oestradiol secretion increased concomitant with the decline in progesterone and before increases in the pulsatile secretion of LH. Therefore, based on this temporal relationship, it is doubtful that an increase in the secretion of LH is the physiological event that initiates the growth of ovulatory follicles during the oestrous cycle in gilts. This hypothesis
Fig. 6. Oestradiol-17β profiles in the utero-ovarian vein and LH and FSH profiles in the jugular vein of Gilt 96-10 from Days 12 through 15 of the oestrous cycle. An asterisk (*) signifies an hormonal pulse according to our statistical definition.

<table>
<thead>
<tr>
<th>Day no.</th>
<th>LH pulses</th>
<th>FSH pulses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Concomitant with FSH</td>
<td>Concomitant with LH</td>
</tr>
<tr>
<td>Total no.</td>
<td>No.</td>
<td>%</td>
</tr>
<tr>
<td>11</td>
<td>15</td>
<td>14</td>
</tr>
<tr>
<td>12</td>
<td>14</td>
<td>13</td>
</tr>
<tr>
<td>13</td>
<td>15</td>
<td>14</td>
</tr>
<tr>
<td>14</td>
<td>31</td>
<td>29</td>
</tr>
<tr>
<td>15</td>
<td>35</td>
<td>34</td>
</tr>
<tr>
<td>16</td>
<td>38</td>
<td>37</td>
</tr>
</tbody>
</table>

Percentages in the same column with different superscripts are different ($P < 0.05$). Pulse data were analysed using analysis of variance procedures for categorical data.
is supported by the observation that the secretion of LH did not change in gilts during natural luteolysis (Guthrie & Bolt, 1990).

Instead of an increase in LH, the reduction in progesterone concentrations at the ovarian level may initiate follicle maturation in pigs. Foxcroft & Van de Wiel (1982) speculated that a component of progesterone's ability to block follicular development in pigs may involve a local inhibition within the ovary. If such an intra-ovarian regulatory mechanism(s) exists, then the rising concentrations of oestradiol on Days 12 and 13 in the presence of waning progesterone secretion may reflect its removal and the subsequent growth of follicles.

In other species, the responsiveness of follicles to gonadotrophin stimuli is enhanced after the fall in progesterone concentrations during luteolysis. Because this phenomenon occurs in the absence of detectable changes in FSH and LH, it is often cited as evidence for a local inhibition of folliculogenesis by progesterone (Kalra & Kalra, 1974; Goodman & Hodgen, 1977, 1983; Goodman et al., 1981). Goodman & Hodgen (1983) proposed that this effect of progesterone on follicular development is mediated via alterations in FSH-dependent events. In the pig, these FSH-dependent events may involve the inhibition and/or stimulation of intraovarian regulators of follicular growth. For example, high intrafollicular FSH removes the inhibitory action of follicle regulatory protein on aromatization and oestradiol production (Tonetta & diZerega, 1990), while it enhances the stimulatory effect of insulin-like growth factors on granulosa cell differentiation and steroidogenesis (Adashi et al., 1985). It is therefore possible that the initial effect of declining progesterone on Days 12 and 13 in our study was a sensitization of the ovary to FSH and/or LH, which caused increased oestradiol production independent of peripheral changes in gonadotrophins.

Alternatively, several studies have demonstrated that an active period of prolactin secretion occurs coincident with luteal regression and the initial increase in oestradiol secretion (Van Landeghem & Van de Wiel, 1977; Dusza et al., 1988). Based on this information, Van de Wiel et al. (1981) suggested that prolactin may participate in steroidogenesis and follicular growth. Prolactin concentrations were not determined in the present study. Therefore, we can make no evaluation of the temporal association between prolactin and oestradiol secretion during luteolysis. However, the administration of prolactin during the follicular phase of the oestrous cycle reduced concentrations of oestradiol, indicating that its effects may be inhibitory rather than stimulatory (Dusza et al.,

### Table 2. Association of oestradiol-17β pulses with a gonadotrophin pulse of both LH and FSH (LH/FSH) from Days 11 through 16 of the oestrous cycle in 13 gilts

<table>
<thead>
<tr>
<th>Day</th>
<th>Total no.</th>
<th>Associated with LH/FSH pulse</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>No.</td>
</tr>
<tr>
<td>11</td>
<td>16</td>
<td>15</td>
</tr>
<tr>
<td>12</td>
<td>34</td>
<td>16</td>
</tr>
<tr>
<td>13</td>
<td>42</td>
<td>20</td>
</tr>
<tr>
<td>14</td>
<td>47</td>
<td>38</td>
</tr>
<tr>
<td>15</td>
<td>61</td>
<td>55</td>
</tr>
<tr>
<td>16</td>
<td>66</td>
<td>61</td>
</tr>
</tbody>
</table>

Percentages in the same column with different superscripts are different (P < 0.05). Pulse data were analysed using analysis of variance procedures for categorical data.
1989). Clearly, the factors responsible for the increase in oestradiol at the onset of luteal regression and before the shift in the episodic release of LH in pigs await further elucidation.

The hormonal profiles of LH and FSH observed in the present study are consistent with the results of previous investigations (Van de Wiel et al., 1981; Foxcroft & Van de Wiel, 1982; Guthrie & Bolt, 1990). In addition, our experiment provides new information concerning the temporal relationship between pulses of LH and FSH during the follicular phase of the pig oestrous cycle. Pulses of FSH not associated with episodes of LH were observed when concentrations of progesterone were elevated on Day 11 and declining on Days 12 and 13. Similar results were observed in cattle (Schallenberger et al., 1984; Walters et al., 1984). However, by Day 14, approximately 90% of the gonadotrophic pulses were composed of concomitant episodes of FSH and LH. One interpretation of these data is that after the removal of progesterone the episodic secretion of LH becomes highly synchronized with that of FSH. Since the frequency of FSH episodes remained consistent from Days 11 through 16, this synchronization was due primarily to the increased frequency of LH release. This explanation seems reasonable based on the well-established inhibitory effects of progesterone on the episodic secretion of LH (reviewed by Foxcroft & Van de Wiel, 1982).

In essence, during the follicular phase of the oestrous cycle, the ovaries were exposed not only to an increased frequency of LH release, but also to an increased number of concomitant pulses of LH and FSH. Studies using cultured granulosa and theca cells from pig follicles support the 'two-cell' theory of steroid production in which both LH and FSH are integrated by follicular cells for oestradiol synthesis (Haney & Schomberg, 1981; Evans et al., 1981). Therefore, it seems appropriate physiologically that the gonadotrophic signal during periods of increased oestradiol production should be composed of pulses of both LH and FSH.

Between Days 14 and 16 of the oestrous cycle, the number and amplitude of oestradiol pulses increased. In fact, hormonal profiles from individual gilts revealed that the preovulatory rise in oestradiol observed in the jugular vein was due to a high-frequency, high-amplitude pattern of secretion from the ovary. Similar observations based on hourly samples were reported by Ciereszko et al. (1989). Also, during this period approximately 90% of the pulses of oestradiol were associated temporally with a pulse of LH/FSH. Our interpretation of these data is that the ovary responded to pulsatile stimuli with an episodic pattern of secretion. Studies with cattle (Walters et al., 1984) and sheep (Baird & McNeilly, 1981; McNeilly et al., 1982) have reported similar relationships between the pulsatile secretion of gonadotrophins and oestradiol.

Although definitive cause and effect relationships cannot be established from our study, the temporal association between episodes of gonadotrophins and oestradiol indicated that from Days 14 to 16 the amount of oestradiol produced may have been dependent on the frequency of gonadotrophin pulses. This could occur in several ways. The enhanced episodic secretion of LH/FSH may have increased oestradiol concentrations by stimulating oestradiol pulse frequency (Baird, 1983). Alternatively, the responsiveness of the follicles to pulses of gonadotrophins may have increased during exposure to a high-frequency pattern (Foxcroft & Van de Wiel, 1982; Walters et al., 1984). Evidence for both these explanations exists in the present study. A positive relationship between gonadotrophin and oestradiol pulses was present from Days 14 to 16. Also, an increase in the amplitude of oestradiol pulses occurred between Days 14 and 15 in the absence of detectable changes in the frequency of LH and FSH episodes.

The present results demonstrate that hormonal profiles of gonadal steroids obtained from sampling the utero-ovarian vein are a more accurate measure of ovarian hormone production than those obtained from the jugular vein. In contrast, the endocrine pattern of gonadotrophins released from the pituitary gland is similar in plasma collected simultaneously from the utero-ovarian and jugular veins. If concentrations of oestradiol in the utero-ovarian vein and gonadotrophins in the jugular vein are used as indices of follicular development and hypophysial secretory activity, respectively, then it is apparent that the growth of follicles during the early stages of the follicular phase is not regulated in the same manner as folliculogenesis just before ovulation. Significant production of oestradiol occurred during luteolysis and before the shift in the episodic secretion of LH. In
contrast, for several days before oestrus oestradiol production was almost exclusively associated with the pulsatile secretion of gonadotrophins. We therefore suggest that during luteolysis follicular growth occurs and factors in addition to LH and FSH are involved with the selection and development of these follicles towards ovulatory competence. However, once the high-frequency, low-amplitude pattern of gonadotrophin secretion characteristic of the later stages of the oestrous cycle becomes established, this endocrine signal is the primary stimulus for the preovulatory production of steroids and growth of follicles.

We thank Dr G. D. Niswender (Colorado State University, Fort Collins, CO) for supplying the LH antiserum; Dr Leo Reichert (Albany Medical College, Albany, NY) for the purified pig LH; Dr R. J. Ryan (Mayo Clinic, Rochester, MN) for the purified pig FSH; and Ms Betty Nichols for secretarial assistance with the preparation of this manuscript.

Contribution from the Missouri Agricultural Experiment Station: Journal Series No. 10993.

References


Kesler, D.J., Garverick, H.A., Youngquist, R.S., Elmore, R.G. & Bierschwal, C.J. (1977) Effect of days postpartum and endogenous reproductive hormones on


Received 20 March 1990