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Involvement of adrenoceptors in the ovarian vascular pedicle in the regulation of counter current transfer of steroid hormones to the arterial blood supplying the oviduct and uterus of pigs

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1 On Day 10 of the oestrous cycle in pigs, after laparotomy noradrenaline (NA), methoxamine (α_1-adrenomimetic, M), Prazosin (α_1-adrenolytic, Pr) in total doses of 4 μmol, and saline were infused (10 min) into the superficial layer of mesovarium on both sides of the ovarian pedicle vasculature, close to the ovary.

2 Blood flow in the ovarian artery, heart rate and progesterone (P_4) and androstenedione (A_4) secretion from the ovary and their concentrations in the ovarian venous effluent, as well as the concentrations of P_4 and A_4 in the blood supplying the oviduct and the uterus, were determined.

3 A significant increase of P_4 and A_4 secretion after NA and M infusion and increased concentrations of P_4 and A_4 in the ovarian venous effluent were found, but these changes did not influence the counter current transfer of hormones from the venous effluent into arterial blood supplying the oviduct and the uterus.

4 Infusion of Pr caused a significant decrease of P_4 and A_4 secretion and their concentrations in the ovarian venous effluent and significantly increased A_4 concentration in the blood supplying the oviduct and uterus.

5 The results indicate that stimulation of α_1-adrenoceptors in the area of ovarian vasculature did not influence, whereas block of α_1-adrenoceptors affected, the local concentration of steroid hormones in the blood supplying the oviduct and the part of the uterus proximal to the ovary, despite the changes in the concentrations of steroid hormones in the ovarian effluent.

Keywords: Adrenoceptors; adrenomimetics; adrenolytics; counter current transfer; steroid hormones

Introduction

The counter current transfer of steroid hormones in the ovarian vascular pedicle of the pig significantly elevates their local concentration in the arterial blood supplying not only the ovary (Krzymowski *et al*., 1981; 1982a,b; 1990) but also the oviduct (Hunter *et al*., 1983; Stefańczyk-Krzymowski *et al*., 1994) and uterus (Stefańczyk-Krzymowska *et al*., 1994). Moreover, the local concentration of progesterone and androstenedione in the blood samples taken from the branch of the uterine artery (which anastomoses with the ovarian artery and supplies the oviduct and uterus) was higher than in the peripheral blood by 35% and 46%, respectively (Stefańczyk-Krzymowska *et al*., 1994). On the other hand, the ovarian and uterine blood flows during the oestrous cycle are temporally associated with the daily ratio of oestrogens to progesterone in the systemic blood (Magness *et al*., 1983; Reynolds & Ford, 1984; Ford & Stice, 1985). The concentrations of oestrogens as well as the ratio of oestrogens to progesterone in the systemic blood are negatively correlated to the ovarian blood flow during the oestrous cycle (Reynolds & Fords, 1984; Ford *et al*., 1985). Progesterone antagonizes the uterine vasodilator effect of oestrogens and enhances vasoconstriction by directly affecting the activity of the periarterial sympathetic nerves and alters the concentration of α-adrenoceptors (Ford & Stice, 1984). Furthermore, catecholamines stimulate the secretion of progesterone in the luteal cells of gilts (Muszyńska, 1991) and in the ovaries of cattle (Kotwica *et al*., 1991b).

This study was conducted to evaluate the effect of a local infusion of noradrenaline, methoxamine (α_1-adrenomimetic), and prazosin (α_1-adrenolytic) on the secretion of steroid hormones (progesterone, androstenedione) in the ovary and their counter current transfer to the arterial blood supplying the oviduct and uterus.

Methods

Animals

Gilts ($n=16$) of similar age (8 months) and body mass (about 110 kg) with two recorded oestrous cycles were mated with a vasectomized boar. The mating day was designated as Day 1 of the oestrous cycle. The experiments were carried out in accordance with principles for the care and use of research animals. On Day 10 of the oestrous cycle, the gilt was premedicated with atropine (0.05 mg kg^{-1} of body mass, Biowet, Poland) and propionylopromazinum (0.5 ml 10 kg^{-1}, Combelen, Biowet, Poland). General anaesthesia was induced with pentobarbitone sodium (12 mg kg^{-1}, i.v., Vetbutal, Biowet, Poland) and maintained with supplementary administration, according to symptoms observed. The reproductive tract was exposed via a mid-ventral laparotomy under aseptic conditions. On both sides of the vascular pedicle, (Figure 1) two silastic catheters (each i.d. 0.6 mm; o.d. 0.8 mm) were implanted into the superficial muscular layer of mesovarium (Figure 1). Catheters were inserted without damaging the ovarian vasculature and fixed to the tissue of the ovarian pedicle.

Three catheters for blood collection were inserted: (a) into the jugular vein according to the method described by Kotwica *et al*. (1978); (b) into the utero-ovarian vein through one

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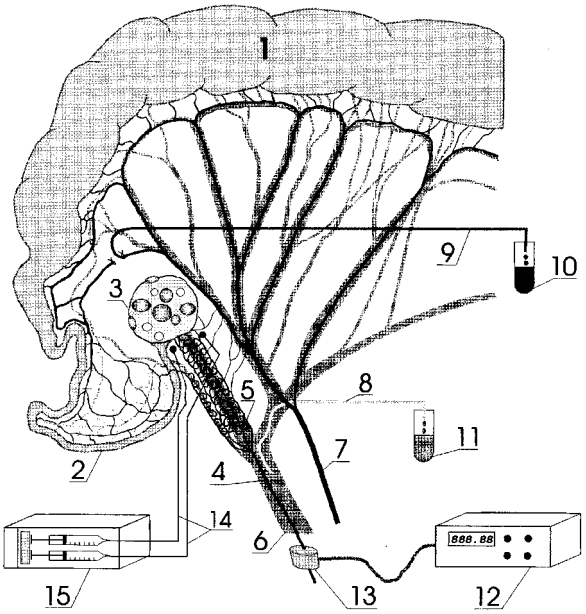

Figure 1 Schematic diagram of the experiment *in vivo* with the infusion of the drugs into the area of the ovarian artery and ovarian vein, measurement of blood flow in the ovarian artery and collection of arterial and venous blood samples for hormone analysis: 1 – uterine horn, 2 – oviduct, 3 – ovary, 4 – uterine artery, 5 – subovarian vascular plexus, 6 – utero-ovarian vein, 7 – uterine artery, 8 – catheter for venous blood collection, 9 – catheter for arterial blood collection, 10 – arterial blood samples, 11 – venous blood sample, 12 – flowmeter, 13 – transducer for blood flow measurement, 14 – catheters for infusion, 15 – infusion pump.

branch of the uterine vein; (c) into the branch of the uterine artery above the anastomoses between branches of the ovarian and uterine arteries.

An electromagnetic transducer for the blood flow measurement (2 mm, Narcomatic, U.S.A.) was implanted on the ovarian artery, 2 cm below its branching (Figure 1). The reproductive tract was replaced in the abdominal cavity in its physiological position and the abdominal cavity was closed. The heart rate was monitored during the experiment by ECG.

Infusion of solfin, noradrenaline, methoxamine and prazosin

All adrenomimetic or adrenolytic substances were diluted in multielectrolytic liquid (solfin). The dose was established in preliminary experiments with noradrenaline. A total dose of 4 μmol infused over 10 min was chosen. This dose decreased blood flow in the ovarian artery by 20%–25% and did not change the frequency of the heart rate. The same concentrations and total doses of methoxamine and prazosin were used. Infusion was started after blood flow stabilization, about one hour after the abdominal cavity was closed. Two ml of multielectrolytic liquid solfin (Polfa, Poland – control group, $n=4$), noradrenaline (Levonor, Polfa, Poland – experimental group I, $n=4$) or methoxamine (Sigma, U.S.A. – experimental group II, $n=4$) or prazosin (Sigma – experimental group III, $n=4$) were infused over 10 min by an infusion micropump (SCAN-1N, Scanelectronics, Warsow, Poland).

Blood flow measurement

The blood flow in the ovarian artery was recorded by an electromagnetic flowmeter (RT 500, Narcomatic, U.S.A.) from 30 min before the infusion until 1 hour after the infusion was started. The mean values of blood flow (ml min^{-1}) for each 5 min period were analysed. The mean blood flow during the last 30 min of the control period (before the infusion) was defined as 100%. The changes in blood flow in the ovarian artery in each group of animals (the control group and the experimental groups) were calculated as a percentage of the mean blood flow found in the control period.

Blood sample collection and determination of concentration of hormones

Thirty minutes before the infusion, and for one hour after the start of the infusion, simultaneous blood samples (approximately 4 ml) from the cannulated branch of the uterine artery, the utero-ovarian vein and the jugular vein were collected every 5 min. The heparinized blood was centrifuged, and the blood plasma samples were stored at -70°C until hormonal assays were completed. The samples were assayed for progesterone and androstenedione by radioimmunoassay procedures previously described in detail (Stefańczyk-Krzymowska *et al*., 1994). The sensitivity of the progesterone assay defined as 93% of total binding was 0.2 ng per tube. The intra- and inter-assay coefficients of variations for these assays were 7.3% and 12.9%, respectively. The sensitivity of androstenedione assay was 79% of total binding and amounted to 5 pg per tube. The intra- and inter-assay coefficients of variations were 7.6% and 13.9%, respectively.

Calculation of the results and statistical analysis

The experiment was divided into three 30-min periods: (A) (-30 to 0 min) before infusion – control, (B) (0 to 30 min) and (C) (30 to 60 min) – after infusion. The results obtained after infusion were compared with the values from the control period. The secretion of progesterone and androstenedione from the ovary was calculated as the mass of progesterone and androstenedione delivered into the blood of the utero-ovarian vein during each min of the experiment. The mean basal secretion of hormones was defined for the 30 min period before infusion (A-control). The changes in secretion are presented after subtracting the mean basal secretion from the values determined for each 5-min period.

The local increase in progesterone and androstenedione concentration in the arterial blood supplying the oviduct and uterus (the branch of uterine artery) was calculated as the difference between the concentration of these hormones in the blood collected from the branch of the uterine artery and in the blood from the jugular vein.

The secretion of hormones from the ovary and the increase of its concentration in the blood of the uterine artery branch were analysed by determining the total area under respective curves (PRISM, GraphPAD, U.S.A.).

The data were examined by analysis of variance and paired t test (ANOVA, INSTAT, GraphPAD, U.S.A.).

Results

Figure 2 shows that local infusion of saline (control group) into the mesovarium area had nol effect on the ovarian blood flow, on progesterone and androstenedione concentrations, or on androstenedione and progesterone concentrations in the blood taken from the branch of the uterine artery.

In the experimental group, the local infusion of noradrenaline into the mesovarium, was significantly decreased blood flow 30 min after start of the infusion (Figure 3a, period C) by 20–25% of mean value for the control period ($P<0.05$). The secretion of progesterone from the ovary increased immediately after start of the infusion (Figure 3b, period B) from 1152 ± 263 to 2210 ± 471 ng min^{-1} ($P<0.01$), and the concentration of progesterone in the ovarian venous effluent rose from 169 ± 36 to 393 ± 83 ng ml^{-1} ($P<0.01$). The secretion of androstenedione rose from 3787 ± 643 to 4705 ± 513 pg min^{-1} (Figure 3b, $P<0.05$) and its concentration in the ovarian effluent from 557 ± 92 to 840 ± 72 ng ml^{-1} in period B ($P<0.05$).

Despite the increase of progesterone and androstenedione concentrations in the ovarian venous effluent, the concentrations of these hormones in the branch of the uterine artery did not increase (Figure 3c).

The local infusion of methoxamine slightly decreased the ovarian blood flow (Figure 4a, $P>0.05$), and significantly increased the androstenedione secretion from 3728 ± 290 to 4918 ± 396 pg min^{-1} (Figure 4b, $P<0.05$). The concentration of androstenedione significantly increased in the ovarian venous effluent from 384 ± 40 to 546 ± 106 pg ml^{-1} ($P<0.05$). Progesterone secretion rose significantly 30–60 min after start of the infusion (Figure 4b, period C) from 1588 ± 287 to 1965 ± 377 ng min^{-1} ($P<0.05$) and the progesterone concentration in the utero-ovarian vein increased from 218 ± 39 to 308 ± 54 ng ml^{-1} ($P<0.05$). The infusion of methoxamine did not influence the progesterone and androstenedione concentrations in the blood supplying the oviduct and uterus (Figure 4c).

Although the local infusion of prazosin did not significantly change the blood flow in the ovarian artery (only the larger fluctuation was observed, Figure 5a), it significantly decreased the secretion of progesterone from the ovary in period C (Figure 5b, $P<0.05$) from 2224 ± 339 to 1309 ± 411 ng ml^{-1}, and its concentration in the ovarian venous effluent (from 203 ± 31 to 139 ± 23 ng ml^{-1}, $P<0.05$). The secretion of androstenedione also fell in this group significantly in period C (Figure 5b, $P<0.05$) from 3391 ± 666 to 2201 ± 410 pg ml^{-1} and the concentration of androstenedione in ovarian effluent

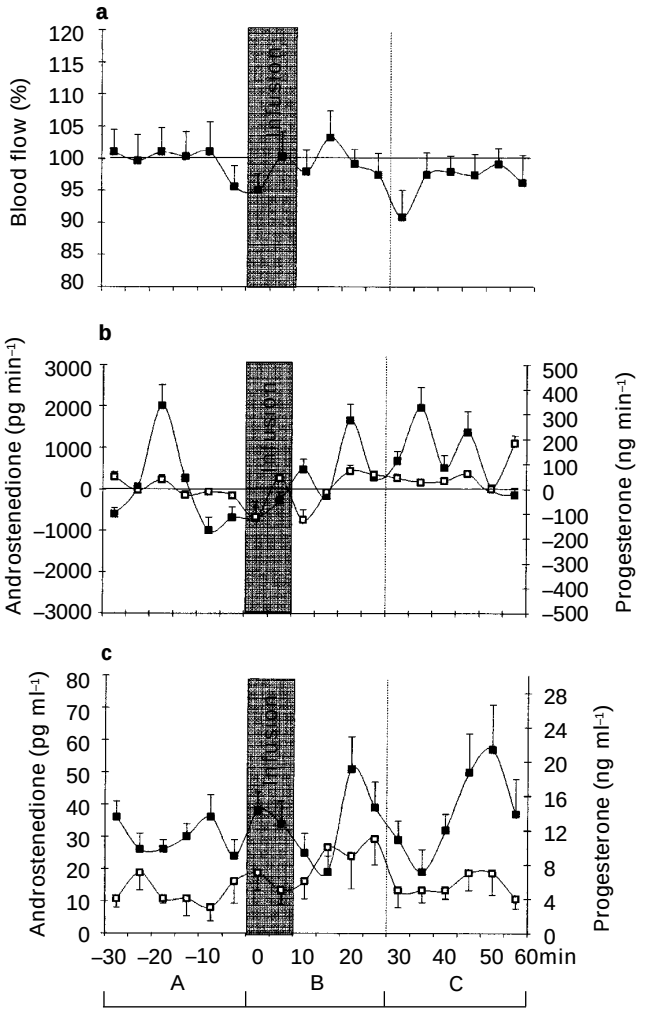

Figure 2 Infusion of solfin. (a) Blood flow in the ovarian artery. Changes of blood flow (mean $\pm$ s.e.) before and after the infusion were calculated in relation to the mean blood flow for the entire group during 30 min before the infusion which was defined as 100%. (b) Progesterone (□) and androstenedione (■) (mean $\pm$ s.e.) secreted from the ovary before and after the infusion. Line 0 gives the basal secretion of the hormones calculated for the entire group during the 30 min before the infusion. The data presented were obtained by subtracting the basal secretion from the values determined for each 5 min period of the experiment. (c) Local increase of progesterone (□) and androstenedione (■) concentrations (mean $\pm$ s.e.) in blood taken from the branch of the uterine artery. The data presented illustrate the differences between concentrations of these hormones in blood taken from the uterine artery branch and the jugular vein. Vertical lines show s.e.

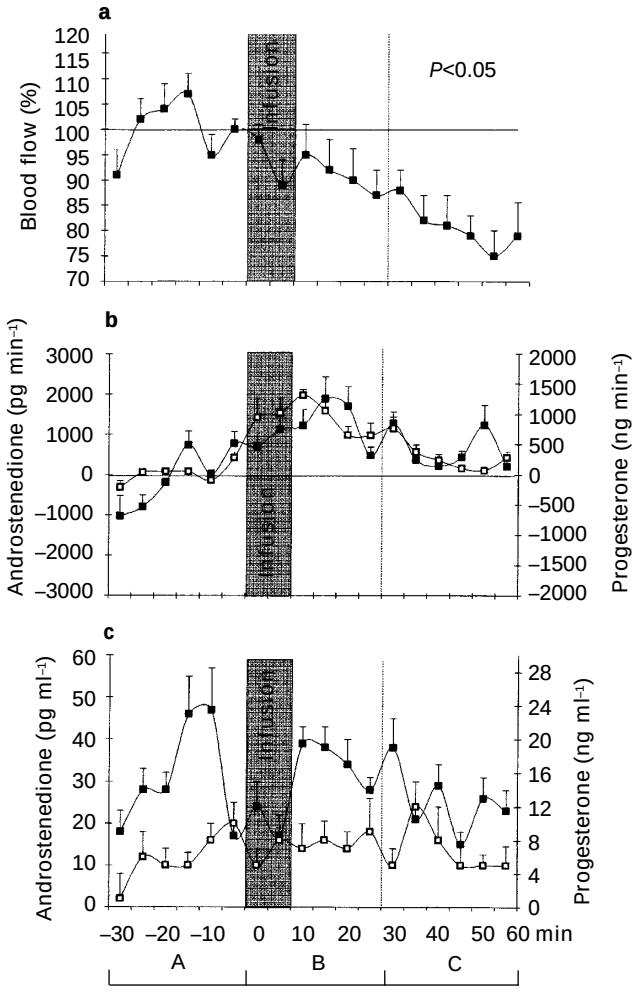

Figure 3 Infusion of noradrenaline. (a) Blood flow in the ovarian artery. Changes of blood flow (mean $\pm$ s.e.) before and after the infusion were calculated in relation to the mean blood flow for the entire group during the 30 min before the infusion which was defined as 100%. (b) Progesterone (□) and androstenedione (■) (mean $\pm$ s.e.) secreted from the ovary before and after the infusion. Line 0 gives the basal secretion of hormones calculated for the entire group during the 30 min before the infusion. The data presented were obtained by subtracting the basal secretion from the values determined for each 5 min period of the experiment. Progesterone and androstenedione secretion increased after the infusion significantly; $P<0.01$ and $P<0.05$, respectively. (c) Local increase of progesterone (□) and androstenedione (■) concentrations (mean $\pm$ s.e.) in blood taken from the branch of the uterine artery. The data presented illustrate differences between the concentrations of these hormones in blood taken from the uterine artery branch and the jugular vein. Vertical lines show s.e.

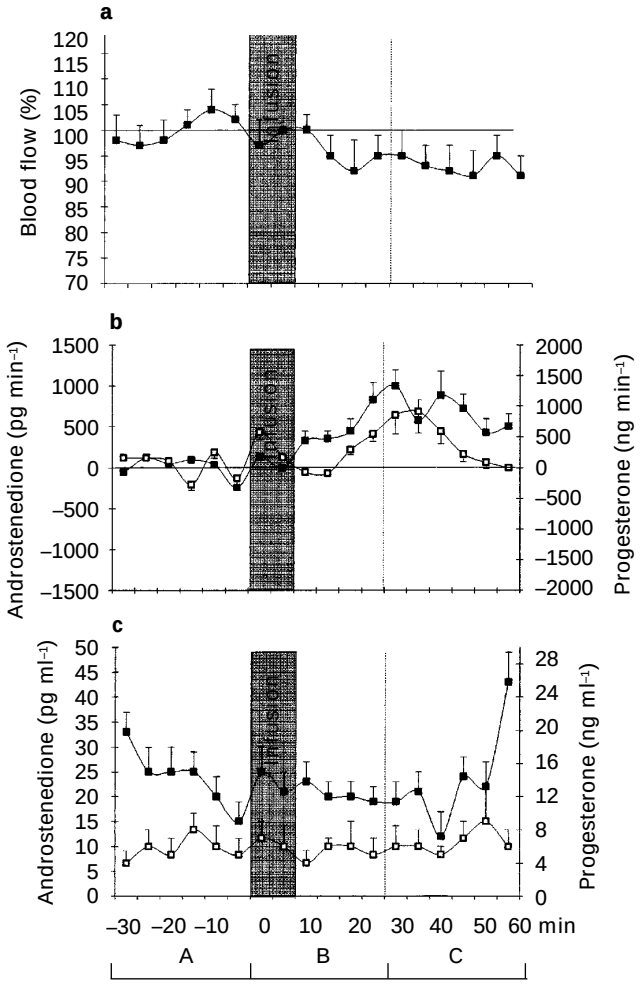

Figure 4 Infusion of methoxamine. (a) Blood flow in the ovarian artery. Changes of blood flow (mean ± s.e) before and after the infusion were calculated in relation to the mean blood flow for the entire group during 30 min before the infusion which was defined as 100%. (b) Progesterone (□) and androstenedione (■) (mean ± s.e.) secreted from the ovary before and after the infusion. Line 0 gives basal secretion of hormones calculated for the entire group during the 30 min before the infusion. The data presented were obtained by subtracting the basal secretion from the values determined for each 5 min period of experiment. Progesterone and androstenedione secretion increased after the infusion significantly; $P<0.05$ for androstenedione during B and C and for progesterone during C. (c) Local increase of progesterone (□) and androstenedione (■) concentrations in blood taken from the branch of the uterine artery. The data presented illustrate differences between the concentrations of these hormones in blood taken from the uterine artery branch and the jugular vein. Vertical lines show s.e.

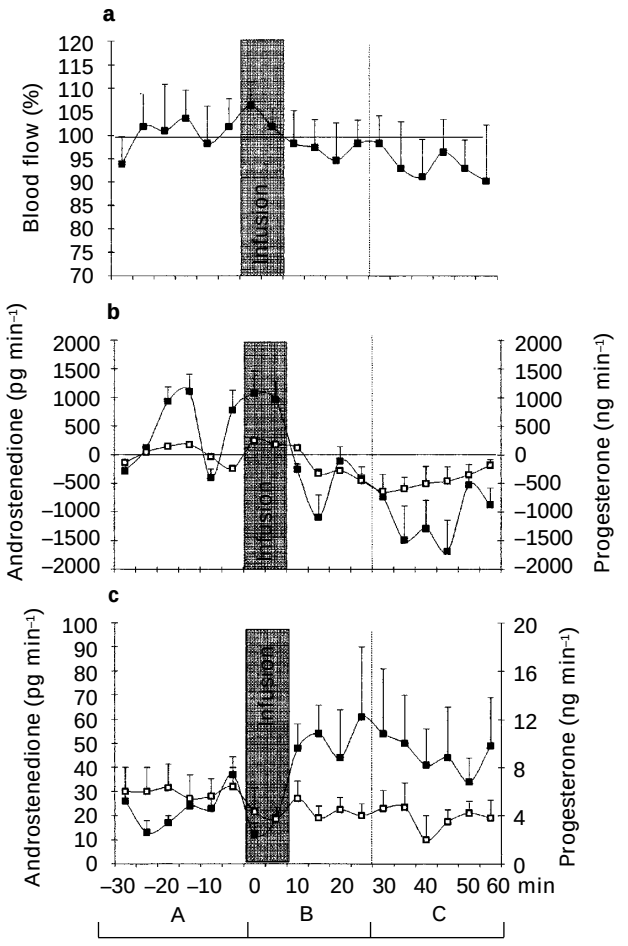

Figure 5 Infusion of prazosin. (a) Blood flow in the ovarian artery. Changes of blood flow (mean ± s.e) before and after the infusion were calculated in relation to the mean blood flow for the entire group during 30 min before the infusion which was defined as 100%. (b) Progesterone (□) and androstenedione (■) (mean ± s.e.) secreted from the ovary before and after the infusion. Line 0 gives basal secretion of hormones calculated for the entire group during the 30 min before the infusion. The data presented were obtained by subtracting the basal secretion from the values determined for each 5 min period of the experiment. Progesterone and androstenedione secretion decreased after the infusion significantly; $P<0.05$. (c) Local increase of progesterone (□) and androstenedione (■) concentrations in blood taken from the branch of the uterine artery. The data presented illustrate differences between the concentrations of these hormones in blood taken from the uterine artery branch and the jugular vein. Local concentration of androstenedione in uterine arterial blood increased after the infusion significantly; $P<0.05$. Vertical lines show s.e.

decreased from 324 ± 71 to 232 ± 45 pg ml^{-1}. The concentration of androstenedione in the blood supplying the oviduct and uterus increased after the infusion of prazosin significantly in periods B and C ($P<0.05$; Figure 5c).

Discussion

The effect of the adrenergic system and the adrenomimetics on the counter current transfer of hormones has never been studied, although a correlation between blood flow and periarterial sympathetic nerve function, as well as between the concentration of adrenoceptors and vasoconstriction, has been demonstrated in the ovarian and uterine vasculature. In this study, with the local infusion of the adrenomimetics (noradrenaline and methoxamine) into the area of ovarian vascular pedicle, a significant increase in progesterone and androstenedione secretion (or release) from the ovaries was demonstrated (Figures 3 and 4). The progesterone concentration in the ovarian effluent after the infusion of noradrenaline was twice as high as before the infusion. This experimental increase in the concentration of the hormone in the ovarian effluent allowed the mechanism of the counter current transfer of the hormones in the mesovarium area to be considered.

The counter current transfer of steroids in the area of the ovarian vascular pedicle in pigs has already been extensively investigated (Kryzmowski *et al*., 1981; 1982a,b; 1990). However, the mechanism for the permeation of hormone from the venous blood and lymph into the arterial blood supplying target organs had previously remained unknown.

It is generally accepted, that the counter current transfer of steroid hormones from the venous blood and lymph into the arterial blood in the mesovarium area depends on the local circulation. Morphological adaptations of the arterial, venous

and lymphatic vessels have been described (Kryzmowski *et al*., 1982b; 1990; Doboszyńska *et al*., 1991; Gawrońska *et al*., 1992). The gradient of the concentration, the facilitated diffusion, or the active transfer have been considered as mechanisms for hormone exchange. The transfer of endogenous testosterone to the arterial blood in the male rhesus monkey was found only in animals with a high endogenous concentration of hormone in the venous blood (Einer-Hensen & Waites, 1977). In contrast to this, the dynamic studies with prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$) in the utero-ovarian circulation of sheep demonstrated a decrease in transfer efficiency when the venous concentration was increased (Land *et al*., 1976) or suggested the facilitated diffusion of $PGF_{2\alpha}$ (Heap *et al*., 1989). Our results showed that in spite of a significant increase in the concentrations of progesterone and androstenedione in the ovarian effluent (induced by infusion of noradrenaline and methoxamine), their concentration in the branches of ovarian artery (anastomosed with the uterine artery) did not rise compared to the control period before infusion (Figures 4 and 5). This indicates that counter current transfer of steroid hormones in the ovarian vascular pedicle is not only regulated by the gradient of concentrations of these hormones. The present results demonstrated that the local infusion of noradrenaline and methoxamine did not change the basal counter current transfer of progesterone and androstenedione from the venous and lymphatic effluent into the arterial blood. It was found that the level of the steroids (progesterone and androstenedione) was permanently higher in the arterial blood supplying the uterus and oviduct than in the peripheral blood. These differences in hormone concentration, typical for the luteal phase (Stefańczyk-Kryzmowska *et al*., 1994) corresponded to control period estimates before the infusion of the adrenomimetics.

On the other hand, the concentration of androstenedione in the branch of the ovarian artery increased after prazosin infusion, despite the considerable fall of androstenedione content in the ovarian venous blood. It is possible that the dilatation and relaxation of the blood vessels in the ovarian vascular pedicle area produced by block of periovarian α_1-adrenoceptors facilitated the counter current transfer of steroid hormones.

The local infusion of noradrenaline in the area of the ovarian vascular pedicle induced a significant decrease of blood flow in the ovarian artery (Figure 3a), whereas neither methoxamine (Figure 4a) nor prazosin (Figure 5a) influenced significantly ovarian arterial blood flow. Moreover, changes in the secretion of steroid hormones were more pronounced after infusion of noradrenaline (Figure 3b) than either methoxamine (Figure 4b) or prazosin (Figure 5b). These differences could be the effect of simultaneous stimulation by noradrenaline of both α- and β-adrenoceptors. An increased secretion of progesterone in bovine corpus luteum after β-adrenoceptor stimulation has been demonstrated previously (Kotwica *et al*., 1991a).

In this study, the method for blood sampling from the ovarian artery through a catheter inserted into the branch of the uterine artery (anastomoses with ovarian artery) was adapted (Stefańczyk-Krzymowska *et al*., 1994). This method was the only one which enabled blood from the branching ovarian artery of the gilts to be collected without damaging the ovarian vasculature, although the blood collected from the branch of uterine artery was a mixture of uterine and ovarian arterial blood. A permanent and significant increase in the concentrations of steroid hormones (progesterone, oestrone, androstenedione) in the branch of the uterine artery anastomosed with the ovarian artery, compared to the systemic blood, has been demonstrated during both the luteal (Stefańczyk-Krzymowska *et al*., 1994) and follicular phases of the oestrous cycle (Stefańczyk-Krzymowska, 1996).

In conclusion, the present results indicate that the factors which stimulate α_1-adrenoceptors in the area of the ovarian vasculature influence the secretion of progesterone and androstenedione from the ovaries but do not change the local concentrations of these hormones in the blood supplying the oviduct and the part of the uterus proximal to the ovary. In contrast, block of the α_1-adrenoceptors in these vessels affected the secretion (or release) of progesterone and androstenedione as well as the concentration of androstenedione in the blood supplying the oviduct and uterus.

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