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DISTRIBUTION OF OESTRONE AND OESTRADIOL IN THE BOVINE OVARY

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Several workers using biological methods have demonstrated the presence of oestrogenic substances in the bovine ovary (see *Velle* 1958). *Adler* (1912) found that extracts of the corpus luteum were lower in oestrogenic potency than were extracts from the remainder of the ovary. *Allen* (1926) found 4.6 rat unites (equivalent to about 380 ng. oestradiol-17 β) per pair of ovaries collected during oestrus whereas ovaries from other phases of the oestrous cycle gave negative response. In follicular fluid, *Zondek* (1926) obtained 700—1300 mouse unites per l. (calculated as oestradiol-17 β : approximately 9—17 μ g. per l. or 9—17 ng. per ml.). *Seemann* (1933) showed that the concentration of oestrogenic substances in the follicular fluid varied with the size of the follicle. *Parkes and Bellerby* (1926) obtained oestrus inducing substances by extraction of young, fluid-containing corpora lutea and found that extracts of pooled corpora lutea gave negative response. In comparing the concentrations of oestrogens in the follicular fluid and in the corresponding residual tissue the higher value was sometimes found in the fluid, sometimes in the tissue.

In a more recent study on the oestrogen levels in the bovine ovary *Duncan et al.* (1955) reported follicular fluid to contain oestrogenic activity equivalent to 130 ng. oestradiol-17 β per ml. and 86 ng. per ml. when ethanolic extracts of the fluid were assayed. Using chemical methods *Velle* (1958) and *Short* (1962a)

were able to demonstrate the presence of oestradiol-17 β , as identified with different chromatographic procedures, in pooled follicular fluid. The results of the quantitative estimates with chemical methods were compatible with the results in bioassays by *Duncan et al.* (1955). In follicular fluid collected from cows during oestrus, *Short* (1962b) found considerably higher concentrations of the same steroid. The major oestrogenic substance normally present in the follicular fluid of the bovine ovary is thus apparently oestradiol-17 β . In addition to oestradiol-17 β relatively small amounts of oestrone have been demonstrated by *Short* (1962a). These two steroids, of which the first has the highest oestrogenic potency, are generally assumed to exist in equilibrium in the tissues.

In man, considerable amounts of oestrone and oestradiol-17 β have been reported to occur in the corpus luteum (*Zander et al.* 1959) and the urinary levels of oestrogens during the luteal phase of the menstrual cycle are comparable to those found during maturation of the follicle. No reliable information seems as yet to be available on the pattern of urinary excretion of oestrogens during the oestrous cycle in the cow. The studies with biological methods indicate that the levels of oestrogens in the corpus luteum of this species are usually low and the luteal tissue thus probably does not contribute much in the ovarian production of oestrogens. However, it can not on the basis of these studies be excluded that the levels of oestrogens in the corpus luteum undergo variations during the oestrous cycle.

The present investigation was undertaken mainly to obtain further informations on the occurrence of oestrogens in the corpus luteum, the follicular fluid and the residual tissue of bovine ovaries of various categories, including i. a. ovaries representing different phases of the oestrous cycle. Rather than processing fluid or tissue from matching ovaries, an attempt has been made to estimate the distribution of oestrogens within single ovaries.

MATERIAL AND METHODS

Ovaries were collected at the slaughterhouse, kept in crushed ice during the transport to the laboratory and then frozen at -20°C . Each pair was kept separately in plastic bags and thawed by placing the bags in water of about room temperature prior to analysis.

Ovaries considered not be representative of any phase of a normal oestrous cycle as well as very large or highly fibrotic organs were discarded. Some cystic ovaries and ovaries collected from pregnant animals (length of foetus: 2—12 cm.) were included in the material.

The corpus luteum was always analyzed separately. The rest of the ovary, or the opposite, was either analyzed as a whole or freed of follicular fluid by means of a graduated syringe.

The tissues were minced with scissors, placed in 50 ml. 2N. NaOH and disintegrated in a blender, care being taken to keep the temperature below 30—40°C. The mixture was left at room temperature for about one hour and then run in the blender a second time. Follicular fluid was admixed with 50 ml. 2N. NaOH and further processed as the tissues, except for the blender treatment.

The alkali was subsequently neutralized by addition of 20 g. NaHCO₃ and the mixture extracted twice with 150 ml. of ether in stoppered plastic bottles. The bottles were centrifuged each time and the ether aspirated into separatory funnels. The ether extracts were further processed essentially according to *Brown* (1955). After washing of the extracts the ether was evaporated and replaced by 25 ml. benzene, 25 ml. light petroleum ether (b. p. 40—60°C) and 25 ml. of 0.4N. NaOH which were poured into plastic bottles, shaken and centrifuged. Extraction of the benzene — light petroleum with water was omitted since it was found that this step, included in the method of *Brown* (1955) to remove oestriol, led to a proportionally greater loss of oestradiol-17 β than of oestrone. The alkali was aspirated with a syringe and the benzene — light petroleum extracted with another portion of 0.4N. NaOH which was combined with the first and submitted to methylation. Methylated material was extracted with n-hexane (*Diczfalusy & Lindquist* 1956) and chromatographed on the alumina column of *Brown* (1955) for the isolation of the 3-methyl ethers of oestrone and oestradiol.

The Kober reaction was performed essentially according to *Ittrich* (1958) and the Kober colour extracted with methylene chloride containing 2 per cent p-nitrophenol. Quantitative estimations were carried out by spectrofluorimetry using a technique developed to minimize interference of unspecific fluorescence and reflected incident light (*Lunaas* 1962).

With the method applied, oestradiol-17 α can not be distinguished from oestradiol-17 β . The 3-methyl ethers of the two epimeric oestradiols are eluted adjacent to each others from the alumina column of *Brown* and have about the same chromogenicity in the modified Kober reaction of *Ittrich*. The predominant oestradiol in the bovine follicular fluid is apparently oestradiol-17 β (*Velle* 1958, *Short* 1962a) but it can not be excluded that the fluid of cysts may sometimes also contain oestradiol-17 α in appreciable proportions (*Velle* 1958). In the present communication "oestradiol" refers to total Kober chromogens of the oestradiol fraction in the chromatographic method of *Brown*, calculated as oestradiol-17 β .

The reagent blank fluorescence corresponded to less than 1 ng. oestradiol-17 β or oestrone which were about the smallest amounts that could be distinguished from zero. The over all sensitivity of the method applied was considerably lower. The recovery of added oestrogens was variable, presumably due to frequent formation of emulsions requiring centrifugation to be incorporated in the extraction procedures. The tendency to form emulsions appeared to some degree to depend on the nature and the amounts of tissue or fluid processed. When 1000 ng. (1 μ g.) of oestrone or oestradiol-17 β were taken through the analytical procedure in the presence of 5 g. ovarian tissue, about 50 per cent could usually be recovered but in some cases the losses amounted to as much as 60—65 per cent. In application of the method to determine oestrogens in porcine ovaries and placental tissue the sensitivity ($P = 0.01$) of single analyses in the range 20—200 ng. oestrone or oestradiol has been estimated to about 5 ng. per g. as calculated from a series of duplicate analyses (*Lunaas*, in press).

RESULTS

The contents of oestrogens in the corpora lutea were generally very small (Table 1). Out of the 36 specimens analyzed only fourteen were found to contain more than 10 ng. oestrone and eleven more than 10 ng. oestradiol. Relatively high values were obtained in a few of the specimens but there were no obvious differences between the amounts of oestrogens found in the corpora lutea of different stages of development or regression. The concentrations of both oestrogens in the luteal tissue tended to be low during the week 2 of the cycle. Out of 4 specimens of

Table 1. Oestrogens in bovine ovaries. Means and ranges of contents (ng.) and concentrations (ng. per g.) of oestrone and oestradiol in corpus luteum and follicular apparatus (including follicular fluid and residual tissue).
Uncorrected values.

	n.	ng.		ng. per g.	
		Oestrone	Oestradiol	Oestrone	Oestradiol
Preovulatory	3	3 — 4 — 30	7 — 5 — 103	1.5 — 1.3 — 27.3	3.2 — 1.6 — 93.3
Week 1 of cycle	9	6.7 (2—14)	8.1 (4—12)	5.9 (0.4—25.8)	6.0 (0.3—17.0)
Week 2	6	7.2 (2—11)	5.2 (3—8)	1.4 (0.3—1.9)	1.0 (0.5—1.3)
Week 3	5	19.9 (6—64)	8.9 (4—17)	4.6 (1.6—15.2)	2.0 (0.9—3.8)
Early pregnancy	9	12.5 (6—38)	11.7 (3—29)	2.4 (1.1—6.3)	2.5 (0.4—6.1)
Cystic corp. lut.	4	18.4 (3—32)	40.1 (12—85)	3.6 (1.3—5.1)	8.5 (2.0—11.8)
Preovulatory	5	165.2 (37—295)	868.2 (230—1130)	27.8 (5.1—56.7)	141.9 (32.0—204.5)
Week 1 of cycle	5	27.5 (8—82)	90.5 (24—248)	4.9 (1.1—12.7)	18.1 (3.2—43.5)
Week 2	7	18.4 (4—31)	62.6 (19—104)	2.4 (0.5—4.3)	8.3 (2.3—16.3)
Week 3	4	29.5 (7—64)	95.8 (17—295)	5.4 (0.7—11.7)	19.3 (5.2—37.5)
Early pregnancy	4	25.2 (9—47)	41.5 (19—88)	4.3 (2.9—6.3)	7.9 (4.0—11.4)
Cystic ovaries	8	229.4 (18—854)	1140.3 (75—4075)	9.7 (0.8—31.6)	44.7 (3.6—150.9)

cystic corpora lutea analyzed, all contained more than 10 ng. oestrone and only one less than 10 ng. oestradiol. In the corpora lutea of early pregnancy the contents of oestrogens were about as the contents of the corpora lutea of the non pregnant animals.

In 43 specimens of fluid from follicles and cysts varying in volume from 0.8 to 29 ml. the amounts of oestrone and oestradiol ranged from 3 to 270 ng. and from 4 to 3400 ng. respectively. The corresponding ranges of concentrations were < 1 –150 ng. per ml. and < 1 –600 ng. per ml. There was no obvious relationship between the amounts or concentrations of oestrogens and the size of the follicle or cyst. The concentration of oestradiol tended to be high in the follicles containing 1.6–2.0 ml. of fluid which included some apparently about to ovulate (Table 2).

Table 2. Concentrations of oestradiol in the fluid of follicles and cysts of bovine ovaries.

Volume of the fluid, ml.	Number of specimens	Oestradiol, ng. per ml.	
		Mean	Range
0.5— 1.0	6	49.5	12.0— 97.9
1.1— 1.5	11	51.6	8.3—133.9
1.6— 2.0	8	273.8	2.4—603.4
2.1— 5.0	5	49.1	1.2—194.3
5.1—10.0	5	32.8	1.8— 84.9
10.0—20.0	4	78.3	0.7—212.9
20.0—30.0	4	29.4	3.3— 80.8

In most pairs of ovaries examined, irrespective of the apparent phase of the cycle, the ovary with the largest follicle contained appreciably more oestrone and oestradiol than the youngest corpus luteum (Table 1). Some of the highest values of both oestrogens were obtained in analysis of ovaries considered to be in the preovulatory state and in cystic ovaries. On the average the total amounts of oestrone and oestradiol were larger in the cystic ovaries than in the apparently normal ovaries about to ovulate whereas the concentrations were usually lower in the cystically enlarged organs.

The percentage oestradiol of the sum total oestrone and oestradiol in the various categories of ovaries was subject of some variation and was found to be highest in preovulatory and in cystic ovaries (Table 3).

Table 3. Per cent oestradiol of the sum total oestrone and oestradiol in the follicular apparatus (including fluid of follicles or cysts and residual tissue) of bovine ovaries.

Ovarian status	Number of specimens	Per cent oestradiol	
		Mean	Range
Preovulatory	5	83.3	77—88
Week 1—3 after ovulation	23	74.7	31—89
Early pregnancy	5	63.8	39—80
Cystic	8	82.5	69—89

In 25 ovaries, including 8 cystic organs, the fluid and the tissue (corpus luteum removed if present) were analyzed separately. The sum total oestrone and oestradiol was most frequently

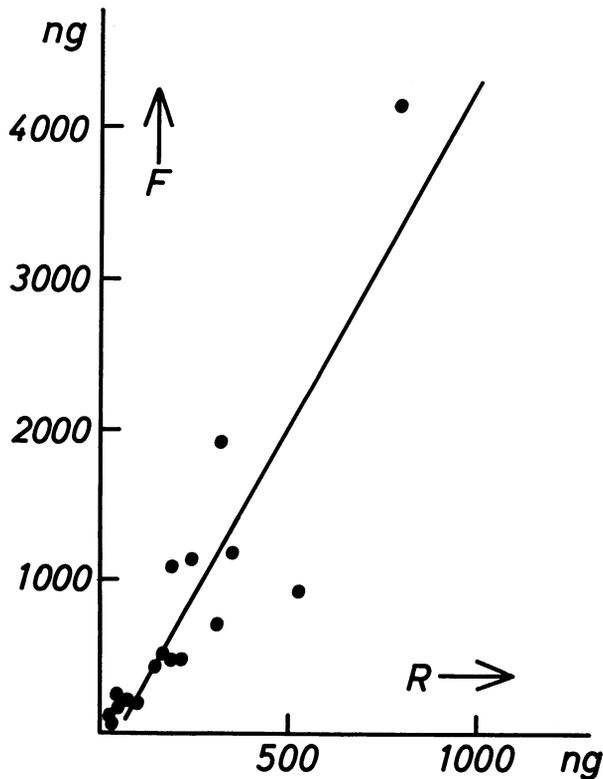


Fig. 1. The relation between the sums total oestrone and oestradiol (ng.) in the fluid of follicles or cysts (F) and in the corresponding residual tissue (R) in bovine ovaries. The coefficient of regression (F on R) was 4.2.

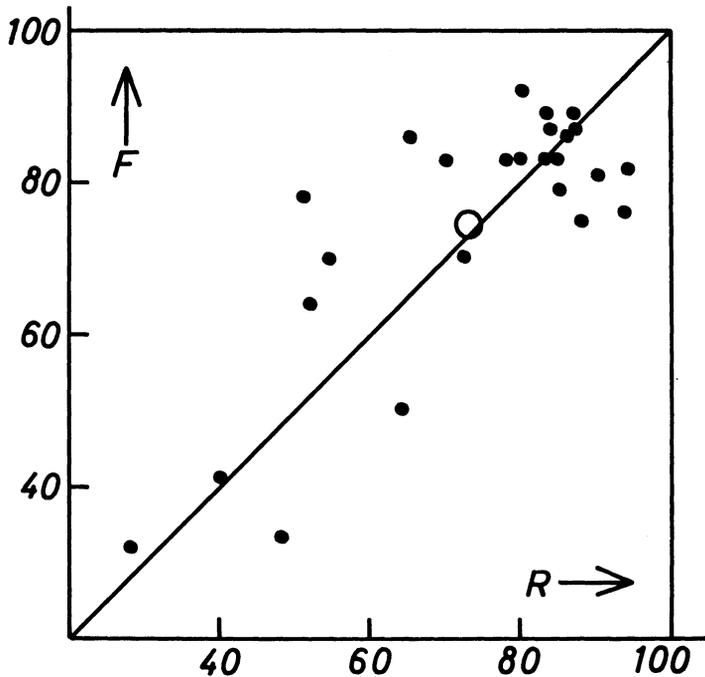


Fig. 2. Per cent oestradiol of the sum total oestrone and oestradiol in the fluid of follicles or cysts (F) and in the corresponding residual tissue (R) of bovine ovaries. Circle indicates the means.

found to be higher in the fluid than in the remainder of the ovary (Figure 1). The values of this sum in the two components of the follicular apparatus were highly correlated ($r = 0.90$).

The mean percentage oestradiol of the sum oestrone and oestradiol amounted to 73.1 (SD = 18.1) in the tissue and was close to the same value in the fluid, viz. 74.5 (SD = 17.3). The percentages of oestradiol in the fluid and in the corresponding tissue (Figure 2) were highly correlated ($r = 0.79$). The mean ratio between the percentages oestradiol of oestrone and oestradiol in the tissue and in the fluid (1.04, SD = 0.18) did not differ significantly from unity.

DISCUSSION

Unconfirmed evidence of increased production of oestrogens in the cow during the luteal phase of the oestrous cycle has been obtained by bioassay of milk (Münch 1954). Also there is a com-

mon experience that cows not infrequently come into heat during the middle of the cycle. This is the phase of the cycle at which the thecal cells of the corpus luteum normally undergo luteinization (*Cupps et al.* 1959). Qualitative alterations in the steroid production could thus be expected to take place in the corpus luteum during the course of its development. In the present investigation no indications were obtained that the fully developed and presumably maximally secreting corpora lutea might contain substantial amounts of oestrone or oestradiol. Rather it appeared that the concentrations of oestrogens were occasionally higher in young and in regressing glands. Since the spread of the values obtained was large, no conclusion seems justified as to possible variations of the luteal tissue levels of oestrone or oestradiol during the oestrous cycle. Neither can much significance be attached to the lower ratio found between oestradiol and oestrone in this tissue than in the follicular apparatus, since it is questionable to which degree the very low absolute values found represented the specific steroids. Other oestrogenic substances do not seem to be present in luteal tissue since studies with biological methods have indicated an oestrogenic potency equivalent only to 1.6 ng. oestradiol-17 β per g. (*Duncan et al.* 1955) which is within the range of values obtained by the chemical method tentatively applied in the present investigation. Further studies are needed to establish if cystic corpora lutea, quite common in the bovine, contain more oestrogens than the compact glands.

No difference could be demonstrated between the levels of oestrogens in the corpora lutea of pregnant and non pregnant animals. In pregnant cows the oestrogenic potency of the luteal tissue has been reported to increase from equaling 0.6 ng. oestradiol-17 β per g. in the interval 1—70 days after conception to 2.7 ng. per g. in the most advanced stages of the gestation time (*Erickson* 1961).

The amounts of oestrogens present in the follicular apparatus as well as the concentrations in the fluid of follicles of various sizes were found to be extremely variable. It is reasonable to assume that the levels of oestrogens in the follicles are depending among other factors on their stage of development or regression and the degree of gonadotrophin exposure. The mean values of oestradiol in the follicular apparatus exceeded those of the corpus luteum at all phases of the cycle. Any signs of oestrogen produc-

tion during the luteal phase should thus probably be ascribed to the growth of follicles known to take place (*Rajakoski 1960*). Contrary to what might be expected from the incidence of heat signs during midcycle, the levels of oestrogens tended to be lower during the week 2 than during the weeks 1 and 3 during which high values were occasionally obtained.

Recently the concentration of oestradiol-17 β has been determined in follicular fluid collected from cows during normal oestrous and after administration of pregnant mare serum gonadotrophin (*Short 1962b*). The values were found to exceed those previously obtained in samples of pooled follicular fluid from ovaries presumably representing all stages of the oestrous cycle by a factor approaching 10 and amounted to 212—836 ng. per ml. (mean: 622 ng. per ml.) as compared to 63.7 ng. per ml. (*Velle 1958*) and 94.0 ng. per ml. (*Short 1962a*). The difference reported here between the total contents of oestrogens in pre-ovulatory ovaries and in ovaries from other phases of the cycle are consistent with these findings. It can be inferred therefore that the ovarian production of oestrogens is increased prior to or during oestrus and it appears that a base level of production, possibly fluctuating, is maintained during other phases.

The contents of oestrogens found in the follicular fluid was relatively high in comparison to the contents of the corresponding residual tissue and these values were highly correlated. Any substantial storage of oestrogens in the ovarian tissue in excess of the amounts present in the follicular fluid thus does not seem to occur, except possibly when the absolute levels are extremely low. From experiments in man (*Peckham & Kiekhofler 1959*) it has been concluded that the follicular fluid is rapidly exchanged. Tritiated water can be demonstrated in the follicular fluid a few minutes after intravenous injection and equilibrium with the plasma water is completed well within one half hour. The follicular fluid may thus be considered a transudate being continuously replaced by exchange of water diffusing past the theca interna and granulosa cells in which the oestrogens are being produced. It appears from the data presented that oestradiol and oestrone are carried into the follicular antrum with this transudate in the same ratio as the steroids exist in the ovarian tissue. The ratio between the two hormones in the ovarian venous blood has as yet not been established but may be assumed not

to deviate much from that in the ovarian tissue and follicular fluid.

The following consideration supports the view that the oestrogens that are present in the bovine ovary are rather rapidly exchanged by release and re-synthesis. The average dose of oestrogens required to induce oestrus in the cow has been estimated to 600 rat unites per day when administered as oestradiol-benzoate to spayed animals (*Asdell* 1946). For the purpose of calculation 600 rat unites can be assumed to equal about 50 μ g. or 50,000 ng. of oestradiol-17 β . The ovarian production prior to or during oestrus should consequently, in rough approximation, increase to about 1000 ng. oestradiol-17 β per $\frac{1}{2}$ hour. This amount is of the same order of magnitude as those found to be present in preovulatory ovaries.

The contents of oestradiol and oestrone in the cysts were on the average higher than in the preovulatory ovaries but the spread was as large as in normal ovaries. Extreme variations in the concentration of oestrogens in the fluid of cysts have been reported previously (*Velle* 1958, *Short* 1962b). Preliminary investigations in this laboratory indicate that similar variations in the fluid levels of oestrogens may occur within the cysts of one ovary or pair of ovaries. Again it seems reasonable that such variations may depend on the age or on the stage of development of the cysts. There does not seem to be any relationship between the oestrogen levels in the fluid and the size of the follicular structure. Any evidence of appreciable storage of oestrogens in the walls of the cysts or that the ratio between oestradiol and oestrone in the tissue and fluid of the cysts should differ from that in normal ovaries was not obtained. The rate of replacement of fluid in the large cysts is presumable lower than in normal follicles but this possible difference would seem not to have any appreciable effect on the distribution of oestrogens within the ovary.

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SUMMARY

The levels of oestrone (oe₁) and oestradiol (oe₂) were estimated with chemical methods in single bovine ovaries of various categories, including ovaries from different phases of the oestrous cycle and from early pregnancy and in cystic ovaries.

In the luteal tissue the levels of the two oestrogens were generally found to be very low.

In the follicular apparatus (including follicular fluid and residual tissue) the oestrogen contents varied considerably and were higher in the preovulatory ovaries (means: 165 ng. oe₁, 868 ng. oe₂) than in ovaries representing other phases of the oestrous cycle (means during the estimated week 1, 2 and 3 after ovulation respectively: 28 — 18 — 30 ng., oe₁ and 91 — 63 — 96 ng. oe₂) and from early pregnancy (means: 25 ng. oe₁, 42 ng. oe₂, foetal length: 2—12 cm.). In the cystic ovaries the contents of oestrogens were higher (means: 230 ng. oe₁, 1140 ng. oe₂) than in the preovulatory ovaries but the concentrations were lower (means: 45 ng. oe₂ per g. as compared to 142 ng. oe₂ per g.).

The means of the ratios between oestradiol and oestrone in preovulatory and in cystic ovaries were almost identical (mean percentages oe₂ of the sum total oe₁ and oe₂: 83.3 as compared to 82.5).

The contents of oestrogens (as oe₁ + oe₂) of the fluid in follicles or cysts were highly correlated with the contents of oestrogens in the corresponding residual tissue ($r = 0.90$) and on the average about four times as large. The percentages oestradiol of the sum total oestrone and oestradiol in the fluid and in the corresponding residual tissue were also correlated ($r = 0.79$).

The concentration of oestradiol (and oestrone) in the fluid of follicles and cysts was extremely variable (0.7—600 ng. per ml.) and was apparently not related to the size of the structures except that the concentration in the fluid of preovulatory follicles tended to be higher than in the fluid of small follicles (containing less than 1.5 ml. fluid) and of large follicles or cysts (2—30 ml. fluid).

ZUSAMMENFASSUNG

Verteilung von Oestron und Oestradiol in Rinderovarien.

In Rinderovarien verschiedener Kategorien, darunter Ovarien unterschiedlicher Zyklusphasen, früher Trächtigkeit sowie zystisch entarteter wurde mittels chemischer Methoden der Gehalt an Oestron (oe_1) und Oestradiol (oe_2) bestimmt.

Der Gehalt der beiden Oestrogene im Lutealgewebe wurde im allgemeinen als niedrig befunden.

Im Follikularapparat (einschließlich Follikelflüssigkeit und Residualgewebe) variierte der Oestrogengehalt beträchtlich und war in präovulatorischen Ovarien höher (Mittel: 165 ng oe_1 , 868 ng oe_2) als in Ovarien anderer Zyklusphasen (Mittel der geschätzten 1., 2. und 3. Woche nach der Ovulation: 28 — 18 — 30 ng oe_1 und 91 — 63 — 96 ng oe_2) und in der frühen Trächtigkeit (Mittel: 25 ng oe_1 , 42 ng oe_2 , Fruchtlänge 2—12 cm). In den zystisch entarteten Ovarien war der Oestrogengehalt höher (Mittel: 230 ng oe_1 , 1140 ng oe_2) als in den präovulatorischen Ovarien, die Konzentration dagegen niedriger (Mittel: 45 ng oe_2 im Vergleich zu 142 ng oe_2 per g).

Die Mittelwerte der Verhältnisse zwischen Oestradiol und Oestron waren in den präovulatorischen und in den zystisch entarteten Ovarien fast identisch (oe_2 als prozentualer Anteil an der Gesamtmenge oe_1 und oe_2 betrug durchschnittlich 83,3 im Vergleich zu 82,5).

Die Oestrogenmengen ($oe_1 + oe_2$) waren in der Flüssigkeit der Follikel und Zysten mit den Mengen im entsprechenden Residualgewebe hoch korreliert ($r = 0,90$) und durchschnittlich viermal grösser. Der Gehalt an Oestradiol als prozentualer Anteil an der Gesamtmenge Oestron und Oestradiol in der Follikel- und Zystenflüssigkeit war mit dem des entsprechenden Residualgewebes ebenfalls korreliert ($r = 0,79$).

Die Konzentration von Oestradiol (und Oestron) in der Follikel- und Zystenflüssigkeit war extrem variabel (0,7—600 ng per ml) und schien in keiner Relation zu der Größe der Strukturen zu stehen, abgesehen von einer Neigung zu höheren Konzentrationen in der Flüssigkeit der präovulatorischen Follikel gegenüber derjenigen in den kleinen (weniger als 1,5 ml Flüssigkeit) und großen Follikeln oder in Zysten (2—30 ml Flüssigkeit).

SAMMENDRAG

Distribusjonen av østron og østradiol i kuovarier.

Ved hjelp av kjemiske metoder ble innholdet av østron (oe_1) og østradiol (oe_2) bestemt i kuovarier av forskjellige kategorier omfattende ovarier fra forskjellige faser av syklus og fra tidlig drektighet og i systiske ovarier.

Innholdet av de to østrogener i lutealvevet blev vanligvis funnet å være meget lavt.

I follikkelapparatet (follikkelvæske og residualvev) varierte østrogeninnholdet betydelig og var høyere i preovulatoriske ovarier (middel: 165 ng. oe_1 , 868 ng. oe_2) enn i ovarier fra andre faser av syklus

(middel i ovarier antatt å være fra henholdsvis 1., 2. og 3. uke etter ovulasjonen: 28 — 18 — 30 ng. oe_1 og 91 — 63 — 96 ng. oe_2) og fra tidlig drektighet (middel: 25 ng. oe_1 , 42 ng. oe_2 , fosterlengde 2—12 cm.). I de systiske ovarier var østrogeninnholdet høyere (middel: 230 ng. oe_1 , 1140 ng. oe_2) enn i preovulatoriske ovarier, men konsentrasjonene var lavere (middel: 45 ng. oe_2 sammenlignet med 142 ng. oe_2 per g.).

Midlene av forholdene mellom østradiol og østron i preovulatoriske og systiske ovarier var nesten identiske (gjennomsnittlig prosent oe_2 av summen total oe_1 og oe_2 : 83.3 sammenlignet med 82.5).

Mengdene av østrogener ($oe_1 + oe_2$) i væsken av follikler og syster var høyt korrelert med mengdene i korresponderende residualvev ($r = 0.90$) og var gjennomsnittlig omtrent fire ganger så store. Innholdene av østradiol som prosent av summen total østron og østradiol i væske fra follikler eller syster og i de korresponderende residualvev var også korrelert ($r = 0.79$).

Konsentrasjonen av østradiol (og østron) i follikkel- og systevæske var ekstremt variabel (0.7—600 ng. per ml.) og syntes ikke å stå i noen relasjon til strukturenes størrelse bortsett fra at konsentrasjonen i væsken fra preovulatoriske follikler tenderte til å være høyere enn i væsken fra både små (mindre enn 1.5 ml. væske) og store follikler eller syster (2—30 ml. væske).

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