Peripheral serum levels of progesterone and prostaglandin $F_{2\alpha}$ during egg transport in superovulated rabbits

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Summary. Concentrations of peripheral serum progesterone and prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$) in superovulated and normally mated rabbits were determined before and after mating by radioimmunoassay. Multiple vaginal washings were also conducted to recover eggs expelled into the vagina of superovulated rabbits. The correlation between the fluctuations of progesterone and $PGF_{2\alpha}$ levels and egg transport in superovulated does was discussed.

The concentration of progesterone remained at low levels before mating, however a temporary increase was seen 10 hours *post coitum* (*p.c.*) and a decrease was noted 24 hours *p.c.* in both normally ovulated and superovulated rabbits. After 36 hours *p.c.* the levels gradually increased in normally ovulated does, while the levels in superovulated does were sharply elevated to reach an equilibrium 78 hours *p.c.*, except for depressions of the levels at 66 and 96 hours *p.c.* Maximum values were observed at 120 hours *p.c.* in superovulated rabbits. During the period of this sharp elevation in progesterone levels, 74.7% of eggs which were recovered from the vagina of superovulated does were obtained.

The concentration of $PGF_{2\alpha}$ in superovulated does showed no significant variations before and after injections of PMSG and HCG, and the levels were relatively constant ranging from 0.8 to 3.7 ng/ml. However, the levels of $PGF_{2\alpha}$ in normally ovulated rabbits greatly varied with time, and it was difficult to discuss their trends.

It was assumed that the expulsion of a number of eggs in superovulated rabbits into the vagina may be due to the post coital sharp elevation of progesterone levels in blood of superovulated does.

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Introduction

The normal egg transport is regulated by the balance of endogenous progesterone and estrogen, and that of exogenous estrogen and/or progesterone caused the disturbance of oviductal egg transport. Thus, an administration of estrogen or progesterone to the rabbit resulted in an expulsion of some of eggs into vagina.^{1,2)} It has been mentioned also that the egg transport in superovulated

rabbits is accelerated,³⁻⁷⁾ and some eggs were found in the vagina of superovulated rabbits at autopsy.⁸⁾ TSUTSUMI *et al.*⁹⁾ reported recently that many eggs were nonsurgically recovered from the vagina of superovulated rabbits during the early hours in pregnancy. However, it was not clear why the eggs appeared into the vagina of superovulated does within such a short time after ovulation. Although HAFEZ, TSUTSUMI and KAHN¹⁰⁾ studied the levels of progesterone in effluent

blood from the ovary in superovulated rabbits, their data were fragmental and were not analyzed in relation to the egg transport. POLIDORO and BLACK¹¹⁾ reported that no significant differences in levels of progesterone in peripheral blood plasma between normally ovulated and superovulated rabbits were seen at 10, 20 and 30 days *p.c.*

The prostaglandins have been shown to alter the oviduct motility and egg transport in rabbits.¹²⁻¹⁸⁾ Significant specific binding of PGE₁ and PGF_{2 α} was demonstrated in the oviduct of both estrous and pregnant rabbits, and PGF_{2 α} binding in the proximal isthmus was significant.¹⁹⁾ Eggs only moved into a particular section of the oviduct when PGF levels in the oviductal tissue declined sharply after reaching a peak value.²⁰⁾ When 5 mg/kg of body weight of PGF_{2 α} was injected subcutaneously in rabbits, 21 to 27 hours *p.c.*, high egg recovery rates (62.6 to 92.7%) were attained by multiple vaginal washings from 1 to 36 hours after injection.²¹⁻²³⁾ However, no precise fluctuations of levels of PGF_{2 α} in the blood of rabbits during the egg transport were demonstrated, although CHALLIS, DAVIES and RYAN²⁴⁾ measured the concentration of PGF in the peripheral plasma during pregnancy.

The present study deals with the concentrations of progesterone and PGF_{2 α} in blood serum of superovulated rabbits, which may affect the *in vivo* egg recovery from the vagina.

Materials and Methods

Animals: Thirty-two Japanese White adult female rabbits weighing 3.3-4.7 kg were used. Twenty of these were injected with 200 IU of PMSG intramuscularly followed by intravenous injection of 100 IU of HCG at

mating 80 hours later, for the induction of superovulation. Twelve animals served as normally ovulated rabbits which received intravenous injection of 100 IU of HCG immediately after double mating with fertile males. Each doe in the superovulation group was bled 9 times sequentially at intervals of 20 to 48 hours mainly. The does were divided into 4 groups, composed of 5 does to each group, and the time of samplings covered from 72 hours before injection of PMSG to 216 hours after injection of HCG, as a whole (Fig. 1). The does in the normal group were bled 6 or 7 times at intervals of 30 to 72 hours. They were divided into 4 groups, composed of 3 does to each group, and the time of samplings ranged from 120 hours before HCG injection to 216 hours after HCG injection. Blood samples (2.5-3.0 ml) were collected from the ear vein using a syringe and after keeping for 6-12 hours at 4-5°C, were centrifuged for 10 min. at 4,000 r.p.m. About 2.0 ml of serum was obtained finally and stored at -20°C until assay. Vaginal lumina of all superovulated does were washed to recover the eggs immediately after bleeding by the *in vivo* vaginal washing method²²⁾ from 40 to 216 hours *p.c.* All does were laparotomized on day 9 or 10, to record the number of corpora lutea and implantation sites. The time of mating was designated as day 0.

Extraction of serum progesterone and prostaglandins: After careful thawing in ice-water, one ml of each sample in a 10 ml stoppered glass centrifuge tube was extracted with 5 ml n-hexan by shaking for 10 min. After centrifugation at 3,000 r.p.m. for 5 min., the n-hexan upper layer containing progesterone was decanted into another tube by freezing the aqueous layer in a dry ice-ethanol mixture. The solvent was removed under a

Fig. 1. Fluctuations in peripheral serum progesterone concentrations in superovulated and normally ovulated rabbits, and in numbers of eggs recovered from the vagina of the superovulated does.

stream of nitrogen at 35–40°C. The residue was utilized as a sample for subsequent chromatographic separation.

The aqueous layer containing the prostaglandin series was acidified to about pH 3 by adding 0.1 ml of 1N HCl and extracted with 5 ml ethyl acetate by strong shaking for 10 min. The ethyl acetate upper layer was transferred into another tube and centrifuged at 3,000 r.p.m. for 10 min. The solvent was then dried under a stream of nitrogen at 50–60°C. The extract was used as the starting material for subsequent chromatographic separation. The recovery rates of progesterone and PGF_{2α} from the serum through extraction and column chromatography were 85.8±2.1% (mean±S.D.) and 83.6±3.0%, respectively.

Progesterone radioimmunoassay: Proges-

terone was separated by a microcolumn of Sephadex LH-20, and the progesterone level was determined by radioimmunoassay following the procedure described by MAKINO²⁵⁾, in which the competitive binding of ³H-labelled progesterone and unlabelled progesterone with antibody against progesterone-3-oxime-BSA were utilized. Figures of the % cross-reaction were 100 with progesterone, 42.6 with 5α-pregnanedione, 6.7 with 20α-hydroxyprogesterone, 1.5 with pregnenolone and 0.9 with 17α-hydroxyprogesterone, respectively. The sensitivity was 25–400 pg of progesterone.

Prostaglandin F_{2α} radioimmunoassay: The E and F series of prostaglandins were separated by silicic acid column chromatography by a modification of the procedure of ORDEN and FARLEY²⁶⁾. The radioimmunoassay of the PGF_{2α} was performed by utilizing the competi-

Fig. 2. Fluctuations of levels of prostaglandin $F_{2\alpha}$ in peripheral serum in superovulated and normally ovulated rabbits.

tive binding of 3H -labelled $PGF_{2\alpha}$ and unlabelled $PGF_{2\alpha}$ with antibody against $PGF_{2\alpha}$. A 3H - $PGF_{2\alpha}$ radioimmunoassay kit (Clinical Assay, Inc., U.S.A.) was used for measurements which were estimated by a modified procedure of CALDWELL *et al.*,²⁷⁾ JAFFE *et al.*,²⁸⁾ and LEVINE and VAN VUNAKIS²⁹⁾. $PGF_{1\alpha}$ cross-reacts 42% with anti- $PGF_{2\alpha}$ serum at the 50% binding level. The cross-reaction with PGF , A, and B is less than 0.02%. The sensitivity was 10-2,400 pg of $PGF_{2\alpha}$.

Results

Concentrations of serum progesterone in normally ovulated and in superovulated rabbits (Fig. 1): Fluctuations of progesterone levels in peripheral serum of normally ovulated or superovulated rabbits from 152 hours before mating to 216 hours *p.c.* are shown

in Fig. 1. Although the mean progesterone levels remained constantly low ranging from 0.35 to 0.37 ng/ml in normally ovulated rabbits before mating, the levels in normally ovulated does were temporarily elevated to 1.6 ng/ml 10 hours *p.c.* and depressed to 0.96 ng/ml 24 hours *p.c.* Thereafter, the levels elevated gradually to reach 4 to 6 ng/ml around the implantation stage. In the superovulated does, the levels of progesterone were elevated slightly from 0.69 to 1.0 ng/ml following PMSG injection, although no significant differences were recognized in the levels before and after PMSG administration. However, temporal elevation (average 4.4 ng/ml, range 2.3 to 8.6 ng/ml) was realized 10 hours *p.c.* and the levels corresponded with that of 120 to 132 hours *p.c.* in the normally ovulated does. After a depression at 24 hours *p.c.*, the

Table 1. Numbers of corpora lutea, implantation sites and eggs recovered from the vagina in superovulated and normally ovulated rabbits

Group		No. of corpora lutea	No. & rate of implantation sites	No. & rate of eggs recovered from the vagina
Superovulation (20 does)	Total	1,222	125	340
	average	61.1± 3.7	10.2± 3.1% ^a	27.8± 5.7% ^a
	Range	35-96	0.0-41.3%	0.0-91.7%
Normal ovulation (12 does)	Total	132	95	
	Average	11.0± 0.5	72.0± 5.4% ^a	
	Range	8.0-16.0	33.3-100.0%	

^a Figures show the percentage to the total number of corpora lutea.

levels of progesterone were sharply elevated to reach 5 to 9 times of the levels in normally ovulated does from 48 to 120 hours *p.c.*, although marked depressions were noted 66 and 96 hours *p.c.* The concentrations of progesterone in superovulated does at 24 hours *p.c.* corresponded to the levels in normally ovulated does around 72 to 96 hours *p.c.* After a remarkable depression in progesterone levels at 96 hours *p.c.*, the levels abruptly increased to 35.6 ng/ml at 120 hours *p.c.* and then were seen varied within the range from 12 to 24 ng/ml till the final blood collection.

Concentrations of serum PGF_{2α} in normally ovulated and in superovulated rabbits (Fig. 2): In superovulated rabbits, the mean concentrations of PGF_{2α} in peripheral blood serum showed no significant differences between the periods before and after injections of PMSG or HCG respectively, although the fluctuations in the levels of PGF_{2α} became larger after HCG injection. The mean levels remained in a range from 0.8 to 3.7 ng/ml. In normally ovulated rabbits, however, the levels of PGF_{2α} greatly varied with the time of sampling. Therefore, it was difficult to document a trend of fluctuations in levels of PGF_{2α}, and to compare the levels of PGF_{2α} in the superovulated rabbits with those in the normally ovulated rabbits. It was not possible to find any relationship between the fluctuations

in progesterone and in PGF_{2α} in both normally ovulated and superovulated rabbits.

Number of eggs recovered from the super-ovulated rabbits (Fig. 1): Total number of corpora lutea, implantation sites and eggs recovered from the vagina were listed in Table 1. The eggs were recovered vaginally from 40 hours *p.c.*, and 92.6% of recovered eggs were obtained concentrically during 54 to 120 hours *p.c.*, especially 74.7% of recovered eggs appeared in vagina from 54 to 78 hours *p.c.* Although most of eggs recovered vaginally by 84 hours *p.c.* were normal fertilized eggs morphologically, the eggs recovered after 96 hours *p.c.* were degenerated (Table 2).

Table 2. Stages of eggs recovered from the vagina of superovulated rabbits during preimplantation stages

Morphology of eggs	No. of eggs	Rate of fertilized eggs (%)
Unfertilized eggs	39 (29) ^a	84.7
4-cell eggs	2	
8-cell eggs	13	
16-cell eggs	31	
32-cell eggs	62 (21)	
Morulae	102 (75)	
Blastocysts	46 (24)	
Degenerating fertilized eggs	32	84.7
Empty zonae pellucidae	13	

^a Figures in parentheses show the number of degenerating eggs.

Discussion

In general, progesterone concentrations in the rabbit ovarian venous blood or peripheral blood rose gradually from the levels in the nonpregnant state and reached a peak at the end of the first third term of gestation; this was followed by a gradual decline during the second third term of gestation and then rapidly declined to reach nonpregnant levels at full term.³⁰⁻³⁶⁾ HILLIARD *et al.*³⁷⁾ claimed that the output of progesterone and its metabolite 20 α -hydroxy-pregn-4-en-3-one (20 α -OH) was elevated immediately after mating or after the administration of gonadotropin which induces ovulation. Their further studies^{38,39)} showed that 20 α -OH secretion by the rabbit ovary increased rapidly following coitus, remained elevated for about 8 hours, and dropped to nondetectable levels by the time of follicular rupture. HILLIARD and EATON⁴⁰⁾ studied *in vivo* release of estradiol-17 β (E₂), 20 α -OH and progesterone from the ovary during preimplantation stages of pregnancy and described that the release of E₂ and 20 α -OH increased following coitus to reach the peak values between 1.5 and 4 hours, but progesterone release remained constant, followed by the decline in these 3 steroids. SPILMAN and WILKS⁴¹⁾ first reported a significant increase in plasma progesterone with time during egg transport. They found that progesterone reached its greatest concentration at 6 hours after mating or HCG injection, and then fell to basal levels at the time of ovulation, and the concentrations began to increase at about 30-36 hours *p.c.* They pointed out the initiation of the postovulatory increase in progesterone secretion corresponds temporarily with the movement of eggs from the ampullary-isthmic junction into the isthmus,

and the progressive increase in plasma progesterone between 30 and 72 hours after the induction of ovulation corresponds to the gradual movement of eggs through the isthmus into the uterus. FUCHS and BELING⁴²⁾ also observed that plasma progesterone, as well as 20 α -OH levels, rose immediately after mating and were maintained at high levels for at least 30 min., and that the concentration of both steroid decreased at 5 hours, returned to postcoital levels 24 hours later, and started to rise on day 5 of pregnancy.

In the present study, progesterone levels that remained very low before mating rose temporarily at the time of ovulation, following a sudden drop at 24 hours *p.c.*, and thereafter increased progressively in both normally ovulated and superovulated rabbits. This trend in fluctuation of progesterone is well agreeable with the observations mentioned above, although marked progressive increment in serum progesterone was realized in superovulated rabbits. The levels of progesterone in superovulated rabbits were higher by 5 to 9 times than that in normally ovulated rabbits from 24 to 120 hours *p.c.* and significant differences were observed between normally ovulated and superovulated rabbits after 40 hours *p.c.* ($P < 0.01$).

While, 74.7% of eggs (254 eggs) recovered from the vaginae of 20 superovulated does were obtained from 54 to 78 hours *p.c.* This period corresponds to the period of the marked elevation of serum progesterone. BOLING⁴³⁾ suggested that progestins secreted prior to ovulation trigger an increase in oviductal muscular contractility, and that the vigorous contractions of oviduct, quite like those seen at the time of ovulation, occur in preovulatory rabbits when the does received injections of progesterone. Our recent observations

showed that an administration of progesterone before and/or at mating caused the acceleration of egg transport and the expulsion of eggs into the vagina.²⁾ Thus, the early appearance of eggs into the vagina of superovulated does may depend on the marked elevation in progesterone levels from 40 to 72 hours *p.c.*

Concerning the effects of prostaglandins on egg transport in rabbits, SPILMAN and HARPER¹⁶⁾ suggested that the F prostaglandins may act to retain the embryos in the oviduct by virtue of their occlusive action, and the E prostaglandins may allow the embryos to pass into the uterus by abolishing tubal occlusion. However, SAKSENA and HARPER²⁰⁾ disagreed with the hypothesis that normal function of the oviduct is regulated by a balance between the effects of PGF_{2α} and PGEs. According to SPILMAN¹⁷⁾, progesterone was more effective than estradiol in decreasing the duration on the response of oviductal motility to PGF_{2α} and the effects of steroid hormones on the response of the oviduct to PGE₁ and PGF_{2α} may contribute to the physiological control of egg transport. Estradiol caused a significant increase in PGF concentrations in the oviduct, ovary and uterus, while by contrast progesterone depressed them to basal levels.²⁰⁾ Uterine sensitivity to PGF_{2α} was also depressed by progesterone administration.⁴⁴⁾ The levels of PGF and PGE in rabbit Graafian follicles increased markedly prior to HCG induced ovulation⁴⁵⁾, and PGF levels of ovulated follicles reached a maximum at the time of ovulation, then quickly decreased⁴⁶⁾. The only report was by CHALLIS *et al.*²⁴⁾ for the concentration of PGF in the blood plasma of pregnant rabbits. The report showed that the mean concentration of PGF was less than 300 pg/ml for much of the pregnancy but showed a significant increase between 21 and 30 days *p.c.*, although no ob-

servations were made on the egg transport. In spite of these evidences mentioned above, the present study failed to show a trend in the fluctuations of PGF_{2α} concentration in relation to the egg recovery from the vagina of superovulated does. This may indicate that an abnormal elevation of progesterone levels in blood of superovulated does shares in an acceleration of egg transport through the reproductive tract, causing the expulsion of many eggs into the vagina, and that the measurement of PGF_{2α} concentration in peripheral blood serum was unfruitful.

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過排卵家兎血中プロゲステロン及び PGF_{2α} 値の変化と卵移動

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最近、我々は過排卵処理家兎の腔を経時的に洗浄した結果、交配後2日目頃から多数の卵が腔に排出されており、さらにこれらの卵の一部は移植によって産子にいたることを確認した。しかし、過排卵処理自体が卵移動を促進するメカニズムは全く不明である。その要因の一つとしては、PMSG 投与による卵胞の過剰発育に伴うステロイド産生の変化が考えられるが、過排卵家兎における

血中ステロイドホルモンの濃度変化についての報告は少なく、また卵移動に関係づけた考察もされていない。本研究では、過排卵処理後に卵移動が促進されることの原因を解明する一助として、血中プロゲステロンと DGF_{2α} の濃度を Radioimmunoassay によって測定した。

無処理交配家兎 (12羽) では、交配前はプロゲステロン値は非常に低い値で推移したが、交配後 10 時間目に

一時上昇後 (1.6 ng/ml), 24 時間目まで低下した。その後、時間の経過とともにゆるやかに上昇したが、交配時から着床時までの値には有意差は認められなかった。一方、過排卵処理家兎 (20 羽) では、PMSG 投与によって血中プロゲステロン値がごくわずかながら上昇したが、交配後 10 時間目で急上昇 (4.4 ng/ml) して、無処理交配家兎の交配後 120~132 時間目と同程度の値を示した。その後、無処理交配家兎と同様に交配後 24 時間目に一度低下したが、48 時間目から 120 時間目にかけての上昇は著しく、無処理交配家兎の 5~9 倍の値に達した ($P<0.01$)。さらに、過排卵家兎の交配後 24 時間目の値は、無処理交配家兎で卵が子宮内に進入するとされている交配後 72 時間目の値に匹敵するか、あるいはそれを上まわっていた。

過排卵家兎の血中 $\text{PGF}_{2\alpha}$ 値は実験期間を通して比較的安定していた (1.2~3.7 ng/ml)。しかし、無処理交

配家兎での $\text{PGF}_{2\alpha}$ 値は変動が大であったため、過排卵処理家兎との比較を行うことは困難であった。

過排卵処理家兎の膣洗浄によって、20羽の家兎から合計 340 個の卵が得られたが (全黄体数 1,222 個に対して 27.9%), 早いものは交配後 40 時間目に回収されており、交配後 54~120 時間目に集中して膣から回収された。この時期は、血中プロゲステロン濃度が急上昇を示した時期と一致し、卵の膣への排出と血中プロゲステロン濃度には明らかに関係があるように思われた。交配後 84時間目までに採取された卵の多くは正常な形態を保っていたが、96時間目以降に採取された卵は全て退化していた。従って、過排卵家兎で卵が交配後の比較的早い時間から膣に排出されてくるのは、排卵後のプロゲステロンの血中濃度の上昇により、卵管内卵移動が促進された結果と推測された。