ENDOCRINE CONTROL OF RECEPTION, TRANSPORT, DEVELOPMENT AND LOSS OF RABBIT OVA*

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Summary. Rabbit ova were transferred to both sides of synchronous pseudopregnant recipients; on one side the ova were transferred to the ovarian bursa to assess the efficiency of ovum reception, and on the other side were deposited within the Fallopian tube to provide information on ovum transport. The recipients were treated with oestrogens, progesterone, or combinations of these hormones. Ova were also transferred to control untreated animals, and to those in which superovulation had been induced. Recipients were autopsied 4 days post coitum, and the ova recovered and examined.

Oestrogen treatment did not influence ovum reception, progesterone produced a slight improvement, and a combination of oestradiol and progesterone gave a greater improvement. Retention of ova in the Fallopian tube was induced by oestrogen treatment, and this effect was opposed when progesterone was given also. Survival rate of blastocysts was reduced by oestrogen treatment especially when ova were retained within the tube. Retained ova had thicker mucin coats. Fewest ova were lost from the reproductive tract in oestrogen-treated animals. Factors affecting rate of pre-implantation embryonic growth are discussed.

INTRODUCTION

The transport of the ovum from the ruptured follicle to the utero-tubal junction is ensured by two series of complex processes: mechanisms for 'reception' or 'adjustment' and mechanisms for tubal 'transport'. Ovum reception is facilitated by anatomical and physiological mechanisms. Tubo-ovarian adjustments are achieved by the ligamentum ovarii proprium, the mesosalpinx and the contractile activity of the fimbriae when engorged with blood. The early and recent work on ovum reception has been extensively reviewed (Hartman, 1939; Hafez, 1959; Westman, 1926, 1959).

The Fallopian tube conducts the ova in one direction and the spermatozoa in the opposite direction, almost simultaneously. Ovum transport is aided by the contractile activity of the tube which is co-ordinated by anatomical, vascular and hormonal mechanisms.

The rate of ovum transport is neither uniform in different species nor in different portions of the tube; the latter was demonstrated in rats (Alden, 1942), rabbits (Chang, 1951), cattle (Schilling, 1958), sheep (Wintenberger-Torres, 1956), swine (Andersen, 1927) and man (Mikulica-Radecki, 1925; Kok, 1926). It is faster in the ampulla than in the isthmus of the tube in the rabbit and probably vice versa in cattle and sheep.

Ovariectomy after mating does not affect the transport rate of rabbit ova but subsequent development is arrested (King, Collins & Peterson, 1932; Adams, 1958). However, a large proportion of ova is retained in the tube as the dose of exogenous oestrogen increases in ovariectomized rabbits (Noyes, Adams & Walton, 1959). Degeneration of the ova following ovariectomy is prevented by treatment with corpus luteum extracts (Allen & Corner, 1928) or progesterone (Pincus & Werthessen, 1938; Adams, 1958).

The rhythmic contractility of the Fallopian tube (Wimpfheimer & Feresten, 1939; Geist, Mintz & Salmon, 1939), and of tubal mucosa (Black & Asdell, 1958), the secretion of tubal mucin around the ovum (Greenwald, 1958), the transport of gametes to the site of fertilization and the tonic restrictiveness of the utero-tubal junction (Noyes, 1959) are all under hormonal control. An appreciation of the hormonal control of reception and transport of ova would facilitate the attempts to modify, either positively or negatively, the natural process of survival and development of the fertilized ova. The objective of this investigation is to study some of these endocrine mechanisms in the intact rabbit with the ovum-transfer technique.

**MATERIALS AND METHODS**

Forty-nine pubertal and fifty-two adult rabbit does of New Zealand Large and Polish breeds, and crossbreds, were used in these experiments. The average weights were 6.3 lb for the pubertal does and 7.5 lb for the adults. The animals were isolated for 16 days before use.

**Donors**

The pubertal does were superovulated by treatment with PMS (Equinex) and hCG (Upjohn) by the technique reported by Hafez (1961). Soon after the injection inducing ovulation, the donors were mated to two fertile bucks. Twenty-two to 26 hr post coitum, the donors were killed and the Fallopian tubes were placed into sterilized Petri dishes. The ova were recovered by flushing the two tubes with a few millilitres of sterilized physiological saline. Then the ova were counted under a stereoscopic binocular microscope (×10), mixed in a watch glass and carefully examined (×45) for their normality. A total of 1102 fertilized (mostly 2-blastomere) supposedly normal ova were selected for transfer into synchronous pseudopregnant recipients.

**Recipients**

The recipients were mated to vasectomized bucks to induce pseudopregnancy which was synchronous to the stage of development of transferred ova. The recipients were anaesthetized with intravenous injection of Nembutal (Abbott).
Laparotomy was performed on both flanks and fertilized ova were transferred to each of the two sides. Then 0.1 ml of penicillin of concentrated solution (100,000 i.u./cc) was sprayed in the abdomen near the site of incision.

In one side, the ova were transferred to the ovarian bursa (Text-fig. 1), while the ovary was in situ in relation to the bursa. Prior to transfer, any excessive peritoneal fluid was removed from the bursa with a pipette. In the other side, the ova were transferred \( \frac{3}{4} \) in. to 1 in. inside the Fallopian tube. The right and left side were used alternately in the series; in five cases, tubal transfer was not performed due to adhesions. The abdomen was closed in one layer with chromic catgut (00) (Ethicon).

![Text-fig. 1. Diagrammatic illustration of the tubo-ovarian relationship in the rabbit. Fertilized ova were transferred with a glass pipette (OB) in the ovarian bursa in one side and in the Fallopian tube in the other side. 1. ovary; 2. infundibulum; 3. utero-tubal junction (intra-mural sphincter); 4. uterus.](image)

**Hormonal treatment**

The recipients were divided into ten groups. In eight groups (Groups I to VIII) the recipients were injected intramuscularly at the time of mating and at the time of ova transfer (24 hr post coitum), with oestrone (Schering), oestradiol benzoate (Schering), progesterone U.S.P. (Abbott), or a combination of oestrogen and progesterone. The hormones were dissolved in sesame oil. In Group IX, the recipients were superovulated with gonadotrophins (as previously described for donors) and mated to vasectomized bucks. Rabbits of the control group (No. X) were not treated with hormones.

Each recipient in the ten groups received fertilized ova in the ovarian bursa in one side and inside the tube in the other side. The groups of recipients were as follows:

- **Group I**, injected twice with 6 µg oestrone (seven recipients)
- **Group II**, injected twice with 18 µg oestrone (five recipients)
- **Group III**, injected twice with 2 µg oestradiol benzoate (five recipients)
- **Group IV**, injected twice with 6 µg oestradiol benzoate (four recipients)
- **Group V**, injected twice with 4 µg progesterone (five recipients)
Group VI, injected twice with 10 µg progesterone (five recipients)
Group VII, injected with 2 µg oestradiol benzoate at mating + 2 µg progesterone at ovum transfer (five recipients)
Group VIII, injected with 2 µg oestradiol benzoate at mating + 10 µg progesterone at ovum transfer (five recipients)
Group IX, superovulated recipients—not injected (four recipients)
Group X, control—not injected (seven recipients)

Autopsy of recipients
The recipients were autopsied 90 to 100 hr post coitum. The reproductive tract was dissected fat free and the ampulla, isthmus and uterus flushed separately. The flushing of each portion were examined microscopically (×45). The native (unfertilized) ova and alien blastocysts were counted, and the intrazonal diameter and thickness of mucin coat of blastocysts were measured with a calibrated micrometric eyepiece. The results were evaluated by the analysis of variance.

RESULTS
OVUM RECEPTION FROM OVARIAN BURSA
The magnitude of ovum reception in this series of experiments was based on the ability of the fimbriae to recover the ova transferred to the ovarian bursa. Ovum reception in each experimental group was calculated as the total number of fertilized ova (alive and degenerating) recovered by flushing, expressed as a percentage to the total number of ova transferred to the ovarian bursa. The native ova (unfertilized), which were recovered also by flushing, were differentiated as being fragmenting or degenerating; such ova were not considered in the data on ovum reception.

In the non-injected recipients (control), 2-blastomere ova were transferred to the ovarian bursa and 7% of these ova were recovered by flushing at 4 days post coitum. The injection of oestrone or oestradiol benzoate did not increase ovum reception as judged by the number of ova recovered by flushing (Tables 1, 2).

Progesterone treatment caused a slight increase of ovum reception from the ovarian bursa as compared to control; the increase was not statistically significant. The average ovum reception was 21% when two doses of 4 µg of progesterone were injected. The average ovum reception was 22% when two doses of 10 µg of progesterone were given. The combination of oestradiol and progesterone injected on 2 successive days caused a significant increase in ovum reception from the ovarian bursa as compared to control. The ovum reception was 26% when 2 µg of oestradiol was followed by 2 µg of progesterone. Average ovum reception was 35% when 2 µg of oestradiol was followed by 10 µg of progesterone.

In the superovulated recipients, the number of corpora lutea on both ovaries ranged from thirteen to twenty-six with an average of twenty-one. The average reception of transferred ova was as low as 4%; in three cases out of four, no ova were picked up.
OVUM TRANSPORT

The efficiency of ovum transport in the Fallopian tube was measured by the proportion of ova flushed from the uterus to the total number of ova recovered from the whole reproductive tract. The calculation included both the native and alien ova. Text-fig. 2 shows that of the ova recovered, larger proportions were obtained in the isthmus of tubes and smaller portions in the uterine horns.

Table 1

<table>
<thead>
<tr>
<th>Hormone injected (μg)</th>
<th>No. recipients</th>
<th>Ova transferred to bursa</th>
<th>Ova transferred to tube</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Native ova</td>
<td>Alien ova</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total No. C.L.</td>
<td>No. ova recovered*</td>
</tr>
<tr>
<td>Oestrone (6 &amp; 6)</td>
<td>7</td>
<td>32</td>
<td>8+ (13)</td>
</tr>
<tr>
<td>Oestrone (18 &amp; 18)</td>
<td>5</td>
<td>38</td>
<td>35+(0)</td>
</tr>
<tr>
<td>Oestradiol (2 &amp; 2)</td>
<td>5</td>
<td>36</td>
<td>10+(4)</td>
</tr>
<tr>
<td>Oestradiol (6 &amp; 6)</td>
<td>4</td>
<td>28</td>
<td>7+(1)</td>
</tr>
<tr>
<td>Progesterone (4 &amp; 4)</td>
<td>5</td>
<td>42</td>
<td>0+(15)</td>
</tr>
<tr>
<td>Progesterone (10 &amp; 10)</td>
<td>5</td>
<td>34</td>
<td>0+(22)</td>
</tr>
<tr>
<td>Oestradiol (2) +</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Progesterone (2)</td>
<td>5</td>
<td>35</td>
<td>1+(15)</td>
</tr>
<tr>
<td>Oestradiol (2) +</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Progesterone (10)</td>
<td>5</td>
<td>34</td>
<td>2+(20)</td>
</tr>
<tr>
<td>Superovulated</td>
<td>4</td>
<td>41</td>
<td>0+(23)</td>
</tr>
</tbody>
</table>

* No. ova recovered from isthmus + No. ova recovered from uterus.

as the oestrogen dose increased. When progesterone was injected in combination with oestrogen, a small portion (6 to 14%) of the ova were retained in the isthmus. In the control recipients and superovulated animals, all the ova were recovered in the uterus.

The average number of ova recovered expressed as a percentage of number of ova (alien) transferred in the Fallopian tube was compared with the percentage recovery of the native ova. The regression line between the two values for the experimental groups was represented (Text-fig. 3) by the equation $\hat{Y} = 24.7 + 0.68 \times X$. The percentage recoveries of alien and native ova were comparable, indicating the validity of technique.
Text-fig. 2. The relative distribution of ova and blastocysts (native and alien) (healthy and degenerating) in the isthmus and uterus of recipients sacrificed 4 days post coitum. The figures in parentheses represent the total number of ova and blastocysts for each group.

Text-fig. 3. Regression showing the degree of accuracy of technique of transfer of ova in the Fallopian tube. Each experimental group is represented by one dot. Each dot represents the average percentage of native ova recovered as related to the average percentage of alien ova recovered in one experimental group. Where the dots are in the shaded area, the percentage recovery of transferred ova was greater than that of native ova and vice versa.
BLASTOCYST SURVIVAL

The survival rate of the blastocysts was based on the number of healthy blastocysts recovered from the recipient expressed as a percentage of the total number of alien ova recovered. In the control recipients, the survival rate of ova was 97%. A similar high survival rate was recorded in groups injected with 10 µg of progesterone or with 2 µg of oestradiol + 10 µg of progesterone; also in superovulated recipient. The lowest survival rate of blastocysts were those of recipients treated with two doses of 10 µg of oestrone, or with 2 µg of oestradiol + 2 µg of progesterone (Table 2, Text-fig. 4).

Different types of blastocyst degeneration such as rupture of zona pellucida and collapse or shrinkage of blastocyst walls were observed in the recipients under oestrogen treatment. This degeneration was more pronounced when the ova were blocked in the tubes. Delayed transport of ova to the uterus was associated with a thick mucin coat around the ova (Plate 1, Figs. 1 to 6).

A certain proportion of the blastocysts was degenerating in animals treated with progesterone or progesterone with oestradiol.

Table 2

<table>
<thead>
<tr>
<th>Hormone injected and dose</th>
<th>Ova transferred to bursa</th>
<th>Ova transferred to tube</th>
<th>Ovum survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. transfers</td>
<td>No. ova transferred</td>
<td>Ovum pickup</td>
</tr>
<tr>
<td>Oestrone (6 &amp; 6) µg</td>
<td>6</td>
<td>67</td>
<td>7</td>
</tr>
<tr>
<td>(18 &amp; 18) µg</td>
<td>5</td>
<td>71</td>
<td>15</td>
</tr>
<tr>
<td>Oestradiol (2 &amp; 2) µg</td>
<td>5</td>
<td>48</td>
<td>15</td>
</tr>
<tr>
<td>(6 &amp; 6) µg</td>
<td>4</td>
<td>70</td>
<td>9</td>
</tr>
<tr>
<td>Progesterone (4 &amp; 4) µg</td>
<td>6</td>
<td>70</td>
<td>21</td>
</tr>
<tr>
<td>(10 &amp; 10) µg</td>
<td>5</td>
<td>54</td>
<td>22</td>
</tr>
<tr>
<td>Oestradiol &amp;</td>
<td>4</td>
<td>46</td>
<td>4</td>
</tr>
<tr>
<td>Progesterone§</td>
<td>5</td>
<td>58</td>
<td>26</td>
</tr>
<tr>
<td>(2 &amp; 2) µg</td>
<td>6</td>
<td>63</td>
<td>35</td>
</tr>
<tr>
<td>(2 &amp; 10) µg</td>
<td>4</td>
<td>46</td>
<td>4</td>
</tr>
<tr>
<td>Superovulated</td>
<td>8</td>
<td>108</td>
<td>7</td>
</tr>
</tbody>
</table>

* Dose at mating and dose at transfer.
† Per cent of number of ova recovered to total number of ova transferred—group average.
‡ Per cent of alien healthy ova recovered from the recipient to total number of alien ova recovered.
§ Oestradiol at mating and progesterone at transfer.

OVUM LOSS

The degree of ovum loss from the reproductive tract was judged by the number of native unfertilized ova recovered when expressed as a percentage to the total number of corpora lutea of the recipients. The highest loss of ova was in the two groups treated with oestradiol. Minimum loss of ova was recorded in recipients treated with 18 µg oestrone (Text-fig. 4).
Fig. 1. A fragmenting native (unfertilized) ovum recovered 95 hr post coitum from the uterus of a recipient. Such ova may resemble the 8- to 16-blastomere ova (×195).
Fig. 2. Two unfertilized native ova in one common mucin coat recovered 94½ hr post coitum from a recipient injected twice with 18 µg of oestrone (×100).
Fig. 3. Blastocyst with ruptured zona pellucida recovered 96 hr post coitum from a recipient injected twice with 18 µg of oestrone. Note the escape of vitellus into mucin coat (×105).
Fig. 4. Blastocyst recovered 96 hr post coitum from uterus of a recipient injected twice with 2 µg oestradiol. At flushing, the blastocyst looked healthy but showed shrinkage prior to photography.
Fig. 5. Degenerating blastocyst recovered 96 hr post coitum from isthmus of a recipient injected with 2 µg oestradiol benzoate at mating + 2 µg of progesterone at ovum transfer (×160).
Fig. 6. Degenerating blastocyst recovered 100 hr post coitum from uterus of recipient transplanted with fertilized ova. Note irregular mucin coat taking shape of a magnifying glass; ten other blastocysts were recovered healthy (×48).

[facing p. 20]
The degree of embryonic development was judged by the intrazonal diameter of healthy blastocysts (including the zona pellucida). The thickness of mucin coat was also measured for the healthy blastocysts recovered under different hormonal treatments. There was no significant effect of hormonal treatment on the diameter of blastocyst or thickness of mucin coat (Text-fig. 5) as revealed by the analysis of variance. However, there was statistical significance between the development of blastocysts in animals treated with 4 to 10 μg of progesterone. In recipients treated with 4 μg of progesterone, the intrazonal diameter of blastocyst was smaller and the thickness of mucin coat was larger than those in animals treated with 10 μg of progesterone. In the group treated with 4 μg progesterone, the intrazonal diameter of blastocysts varied from 165 to 479 μ with an average of 281 μ; the thickness of mucin coat ranged from 17 to 132 μ with an average of 78 μ. In the group treated with 10 μg of progesterone, the intrazonal diameter of blastocysts ranged from 248 to 776 μ with an average of 528 μ, the thickness of mucin coat varied from nil to 99 μ with an average of 33 μ.

DISCUSSION

In a preliminary experiment (Hafez, unpublished data), fertilized ova were transferred in the peritoneal cavity but outside the ovarian bursa and as close
as possible to the fimbriae; none of the ova was picked up by the fimbriae. Intraperitoneal insemination was reported in a few species. Unlike the spermatozoon, the ovum does not exhibit potential motility and it seems improbable that intraperitoneal ovum transfer will be feasible.

The technique of ovum transfer in the ovarian bursa of the rabbit provides a comparative method to evaluate the magnitude of ovum reception by the fimbriae. Although the percentage of ovum pickup from the ovarian bursa was low in the untreated animals, the method seems to be satisfactory for comparison between different hormonal treatments. It has been shown that the

![Text-fig. 5. Development of blastocyst and hormonal treatments. The figure illustrates the range (shaded rectangulars) and mean (dotted lines) of the intrazonal diameter and thickness of mucin coat of all healthy blastocysts.](image)

functional activity of the fimbriae in picking up the ova from the ovarian bursa can be modified by exogenous steroid hormones. At a given dosage level of injected hormone, the number of ova picked up from the ovarian bursa varied widely between animals. Table 2 shows that as the dose of oestrogen was increased, the proportion of ova picked up from the ovarian bursa did not decrease.

Many of the mechanisms of reception and transport of ova are markedly affected by the complex actions and interactions between the ovarian steroid and posterior pituitary hormones, the sympathetic nervous system, and the adrenal steroids (Szego & Roberts, 1953). That some regions of the tubal musculature may be subject to hormonal action and so affect movement of the ovum has been indicated by Burdick, Emerson & Whitney (1940). The ova
may be tube-locked with oestrogen injection of proper dosage (Burdick & Pincus, 1935) or accelerated in cases of superovulation (Wislocki & Snyder, 1933).

The injection of 2 µg of oestradiol benzoate did not result in the normal transport of the ova. However, the tendency of ova to be transported at a normal rate increased when the dose of oestradiol was increased to 6 µg. It is suggested that ovum passage from the tube to the uterus is influenced to some extent by the tonus of the utero-tubal junction. The latter in turn is under hormonal influence. In the present study, it has been shown that oestrogen treatment delays the transport of ova to the uterus. It is not known whether the progesterone accelerates the ova since the recipients were autopsied at a time when all the ova are normally in the uterus. In the rabbit, there is no unequivocal evidence that increased levels of progesterone, whether derived from exogenous or endogenous sources, accelerate the passage in the tube (Adams, 1960). However, there is evidence of such mechanisms in the cow (Dowling, 1949) and sheep (Robinson, 1951).

It may be concluded from the present results that tubal motility of the right degree of intensity is a most important factor for normal rate of transport. The implication is that active tubal motility delays ovum transport while quiescent motility favours rapid transport through the tube. The irregularity of the rate of passage of individual ova and of groups of ova through the tube and uterus suggests that the contractile activity of these organs is highly dyskinetic when they are under the control of oestradiol benzoate alone (Noyes, 1959).

The survival of rabbit morulae declines when their transport through the utero-tubal junction is delayed. Although early blastocysts could be recovered from the isthmus, the tubal environment is unfavourable for any further development. In other species, such as the cat, if the ova are locked in the tube, they develop into healthy blastocysts (Amoroso, 1956). Although the functional state of the tube is conditioned by the ovarian hormones, the transport of the ova and early embryonic development in some species are not dependent upon them. In the cat, double oöphorectomy after ovulation prevents neither the transport of ova nor pre-implantation development of embryo (Amoroso, 1956).

In the different experimental groups, there was no statistically significant difference between the intrazonal diameter of the blastocyst or the thickness of mucin coat; this is mainly due to the wide individual differences within the same animal. Beatty (1958) has demonstrated that the size of blastocyst varies greatly within the uterine horn and that the variation in mean blastocyst size between different does is not related to mature weight or age of doe. Text-fig. 5 shows that there was a trend for the diameter of blastocyst to increase and the thickness of mucin coat to decrease as the level of progesterone (endogenous or exogenous) increases. However, Lutwak-Mann (1956) reported that blastocysts collected at 6½ days from superovulated does numbering up to twenty per uterine horn, did not differ in weight at this stage from ordinary blastocysts. Further studies are needed on the effect of exogenous hormones on cleavage rate of fertilized ova. The degree of blastocyst expansion, in turn,
influences the thickness and shedding of mucin coat. Venge (1950) transferred ova with thin, medium and thick mucin coat in order to ascertain any possible interdependence between thickness of mucin coat and the number of foetuses. In 'large race' rabbits, there was a difference in the percentage of foetuses between the three classes; ova with a medium mucin coat giving a larger number of foetuses \( P < 0.01 \). In the Polish breed (small adult size) there was no definite trend. The rate of blastocyst development may be affected by genetic factors since there are breed differences in the rate of early cleavage of fertilized ova. The percentage of 4-blastomere ova recovered 25 hr post coitum was higher in the 'small race' than in 'large race' (Venge, 1950).

In the present study, the loss of transferred ova is due to \((a)\) the natural hazards causing loss in the first 4 days of pregnancy in unoperated females of the recipient stock (in operated females, the transferred ova are presumably as much exposed to these hazards as are the native ova) and \((b)\) the technical hazards arising from the procedure of transfer which cause additional loss of transferred ova. Technical hazards may cause whole-inoculum loss, partial loss of inocula through injury or escape of some of the ova, and reduction of blastocyst number owing to surgical interference. In mice, whole-inoculum losses were estimated to account for about 33% of all ova injected (McLaren & Michie, 1956). Runner (1951) seems to have encountered a similar phenomenon in transfers of unfertilized ova to the ovarian capsule.

It may be concluded that the hormonal requirements of reception, transport, development and survival of fertilized ova are not identical. A certain oestrogen : progesterone ratio is essential for each of these links in the chain of events. The effect of exogenous hormones on the reception, transport and survival of ova is so variable; this may be due partly to variation in the initial levels of endogenous hormones and/or differences in the degree of sensitivity of tissue to hormones.

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Hormones and fate of rabbit ova


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