ANIMAL EXPERIMENTATION

Fimbrial Capture of the Ovum and Tubal Transport of the Ovum in the Rabbit, with Emphasis on the Effects of β_2 -Adrenoreceptor Stimulant and Prostaglandin $F_{2\alpha}$ on the Intraluminal Pressures of the Tubal Ampullae

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Purpose: Our purpose was to elucidate the roles of the ampullar and isthmic portions of the oviduct and the effects of drugs on oviductal contractility.

Methods: Prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$; Ono Pharmaceuticals, Osaka) and oxytocin (Atonin-O; Teikoku Hormone Manufacturing Co. Ltd., Tokyo) were used to stimulate oviductal contractility, and ritodrine hydrochloride (Utemerin; Solvay-Duphar Corp., Denmark) to inhibit the contractility.

Results: Both $PGF_{2\alpha}$ and Atonin-O were involved in ovum capture by the ampullar oviduct by stimulating contractility, thus altering the intraductal pressures. Utemerin is effective in inhibiting the enhanced contractility induced by $PGF_{2\alpha}$ and Atonin-O.

Conclusions: Variations in pressure of the ampullar portion of the oviduct seem necessary for the capture of ova expelled from the ovary. Once in the isthmic portion of the oviduct, transport appears to be under the influence of ciliary activity rather than variations in contractility.

KEY WORDS: ovum capture; ovum transport; intratubal pressure; β_2 -adrenoreceptor stimulant; prostaglandin $F_{2\alpha}$.

INTRODUCTION

Progress in assisted reproductive technology has necessitated intensive study of fertilization and the development of the zygote. Thus, the role of the fallopian tubes and the specific functions of tubal physiology have become of great interest. The tubes are known to be important for the transport of sperm, nurturing of the ovum, fertilization, and the subsequent development and transport of the zygote prior to nidation.

The fimbria in rabbits at the time of ovulation approach the ovaries and envelop the expulsion site. During laparoscopic observations a similar phenomenon has been observed in humans. This phenomenon is considered to be of importance in the capture of the ovum. However, the definitive mechanisms involved in causing the increase in fimbrial motility, and its envelopment of the expulsion site and active capture of the ova and follicular fluids, have not as yet, been adequately clarified. The fimbria demonstrate an increase in activity near ovulation. It has been reported that during the follicular phase, the activity in the ampullary portion of the tube is enhanced. The mechanisms involved in the capture and transport of the ovum can easily be associated with the observed phenomena of enhanced smooth muscle activity in the ampullaris and fimbria, together with the smooth muscle contractions of the ampulla at ovulation (1,2).

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This investigation involves the serial measurement of intrafallopian tubal pressures during the periovulatory period, using a calibrated pressure analog adapter inserted into the tubal lumen. This project was designed to investigate tubal activity in the periovulatory period, the effects of various drugs on either the stimulation or the inhibition of tubal activity, and their role in ovum capture and transport. Our test animals were domestic Japanese white rabbit females and the materials tested were β_2 -adrenoreceptor stimulant, Utnerin, prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$), and Atonin-O.

MATERIALS AND METHODS

The test animals were female white Japanese rabbits weighing 3.0–3.5 kg. Automated signaling devices were installed under intravenous anesthesia to measure serial tubal activity and pressure. The rabbits were allowed a recovery period of 2–4 weeks to allow a return to physiologic responses. The telemetry system used (a) an implantable miniature transmitter which continuously senses, processes, and transmits information from within the animal (Data Sciences, Inc., USA); (b) a receiver located within or near the cage (Data Sciences, Inc.); (c) a recording system (NEC-Sanei TR41); and (d) a computer-based data acquisition system which collects, displays, and stores the telemetered data (Data Quest 3). The transmitters comprised of a sensor, an amplifier, a transmission circuit, and a battery, contained in a round 20-mm-diameter $\times$ 3-mm-thick component, and were anchored subcutaneously. The life span of these transmitters was roughly 2 months. The pressure sensors consisted of a urethane catheter, 2 mm in diameter, which was anchored centrally in the lumen of the ampullary portion of the tube via an abdominal route and the sensor inserted into the fimbrial ostium and plugged with a biocompatible gel to prevent invasion by abdominal fluids. The catheters were filled with a noncompressible fluid. The pressure gradients sensed at the plugged ends were automatically transmitted to the telemetry monitor. To reduce trauma and minimize adhesion formation, all procedures were performed by microsurgical techniques using 10–0 or 9–0 nylon sutures. Transmitted signals were received and amplified with a bioelectric amplifier (NEC-Sanei 1253A) and recorded by a pen recorder and date recorder (NEC-Sanei 7R41). The signal recorded on the data recorder was analyzed by a computer system (NEC-Sanei signal processor

7R18), underwent analog–digital conversion, and was then submitted to a fast Fourier transform (FFT).

Ovulation was induced with 100–150 IU of human chorionic gonadotropin (hCG) injected into a vein of the ear. We attempted to determine whether the phenomenon of ovulation instigated or induced an increase in tubal contractility to synchronize with the expulsion of the ovum to enhance ovum capture. The rabbits were injected with 100–150 IU of hCG in a 1-ml bolus intravenously (i.v.) into an ear vein to induce ovulation.

Following the hCG injection, we investigated the effects of Utnerin and $PGF_{2\alpha}$ on ovum capture. We administered Utnerin in 1-mg doses intramuscularly (i.m.), starting 90 min prior to the estimated time of ovulation in hCG-primed rabbits (10 hourly injections). After the last injection of Utnerin, we laparotomized the rabbits ($N = 5$) and dissected out the fallopian tubes, taking care to remove the ampullae and isthmic portions separately. We then carefully lavaged the tubal portions with physiologic saline to determine whether any ova had been captured and transported. Another group was injected with Utnerin as above, then injected with 1 mg of $PGF_{2\alpha}$ four times (30, 90, 150, and 210 min postovulation), and examined as above ($N = 5$).

We then investigated the effects of Utnerin on the transport of ova in the tubes. This was performed in three groups of rabbits ($N = 5/\text{group}$). The first group was injected with 1 mg of Utnerin hourly (44 injections), starting 1 hr postovulation. The second group had their first injection 6 hr postovulation, and the third group received their first injection 12 hr postovulation. All three groups received a total of 44 hourly injections to maintain uniformity of conditions. The tubes were carefully dissected to evaluate the degree of ovum transport. The ampullae were severed at the ampullar–isthmic junction (AIJ), then the isthmic portion was carefully trisected, the most distal portion being from the AIJ to the free isthmic portion. The midportion was free isthmic tissue, and the medial portion was free isthmic tube to the isthmic–uterine junction (IUJ). The uterine cavity and all four segments were carefully lavaged with physiologic saline and evaluated for the presence or absence of ova.

As controls, we evaluated the effects of Utnerin and Atonin-O on tubal contractility on rabbits which did not receive hCG. The rabbits ($n = 5$) received either Atonin-O or $PGF_{2\alpha}$ as a simple bolus, and the changes in intratubal pressures were evaluated.

RESULTS

In a control series ($N = 5$), we investigated the effects of Utererin, Atonin-O, and $\text{PGF}_2\alpha$ on intact tubes without hCG-induced ovulations. Both Atonin-O (0.015 IU/kg i.v.) and $\text{PGF}_2\alpha$ (0.015 mg/kg i.v.) caused a marked increase in tubal activity, as seen in the telemetered recording. Utererin (0.15 mg/kg i.v.) administered during the stimulated condition caused a rapid inhibition to baseline pressures (Fig. 1).

To determine whether the increased tubal activity was in synchrony with ovulation, we continuously monitored tubal intraluminal pressures from after hCG administration until after ovulation had occurred. The intratubal pressures were 4.8 ± 2.2 mm Hg ($N = 5$). This condition remained stable until 9.5 ± 1.6 hr ($N = 5$) post-injection of hCG, at which time a marked reduction in pressure was noted. Thus, a rapid drop in ampullar pressure appears to occur just after ovulation, suggesting a response in reaction to the ampullar tissues being exposed to follicular contents. It is believed that this drop in ampullar pressure results in drawing the ovum into the ampulla from the abdominal cavity. This was followed by a rapid recovery. Intratubal pressures then increased to 11 ± 5.2 mm Hg ($N = 5$), and there was a disparity between contractions and relaxations. This enhanced activity continued for roughly 5 min, after which intratubal pressures returned to control conditions. Subsequently, there was

about 20 min of periodic light variations in tubal pressure, accompanied by increased tubal contractions.

The information telemetered from the rabbit tubal ampullae indicated a surge in tubal activity coincident with ovulation. Figure 2 shows the response elicited in one rabbit. Our data suggest, from the evidence of variations in intratubal pressures, that this rabbit ovulated three times. Responses were recorded serially following the intravenous injection of hCG. Figure 3 shows the power spectrum of the tubal intraluminal pressure gradients of the rabbit ampulla.

The effects of $\text{PGF}_2\alpha$ and Utererin on ovum capture were as follows: (a) Utererin, 1 mg i.m., was administered hourly seven times, starting 90 min before ovulation ($N = 5$). We observed 8.6 ovulations. However, on examining the ampullae and isthmic portions of the tube, we were unable to detect the presence of ova, suggesting that Utererin was successful in inhibiting ovum capture by the ampullae. (b) In another group ($N = 5$) treated with Utererin as above, we injected $\text{PGF}_2\alpha$, 0.015 mg/kg i.v. hourly, three times, starting 30 min postovulation. We detected an average of 7.4 ova per rabbit, from an estimated 8.2 ovulations, indicating that $\text{PGF}_2\alpha$ overrode the effects of Utererin and resulted in a 90.2% ovum capture.

The effects of Utererin on ovum transport in the fallopian tubes were as follows: (a) In the group ($N = 5$) which received Utererin, 1 mg hourly, 44 times, starting 1 hr postovulation, we identified 19

Fig. 1. Tubal intraluminal pressure gradients in response to $\text{PGF}_2\alpha$ and Utererin of the rabbit ampulla. The upper tracing is a control response, showing no apparent reaction other than the normal pattern with no drug effect. The middle tracing shows that both $\text{PGF}_2\alpha$, 0.015 mg/kg i.v., and Atonin-O, 0.015 mg/kg i.v., show similar responses, manifested by increased tubal contractility. The lower tracing shows the effects of Utererin, in which the increased contractility is inhibited and the tubal responses return to the pattern seen in the controls.

Fig. 2. Tubal intraluminal pressure gradients at ovulation of the rabbit ampulla. The upper panel shows the overall response to a bolus injection of hCG. The lower panel is a magnification of the ampullar response at ovulation. As can be seen, a drop in intraluminal pressure is seen before ovulation, which is signified by an increase in pressure.

ovulation sites on the ovaries. In the ampullae we detected 4 ova (21%); and in the isthmic portion of the tube, 11 ova (57.9%). (b) In another group ($N = 5$), we performed the same number of Utnerin injections (44) starting 6 hr postovulation. In this group

we detected 17 ovulation sites and 12 ova in the mid-portion of the isthmic tube (70.6%). However, in this group, no ova were detected in the ampullae. (c) In the third group, with the first injection 12 hr postovulation (44 times) ($N = 5$), we identified 10 ovulations,

Fig. 3. Power spectrum of tubal intraluminal pressure gradients of the rabbit ampulla. The power spectrum analysis following a bolus injection of hCG, 50 IU/kg i.v., shows that rabbits ovulate at roughly 10 hr subsequent to the hCG administration. This power spectrum represents the patterns observed during multiple ovulations, the first occurring at 9 hr 58 min after the hCG injection.

with 4 ova in the medial isthmic portion and 4 ova in the uterine cavity, but with no ova in the distal isthmus or ampullae.

Our observations in the three groups receiving Utemerin postovulation revealed a marked inhibition of tubal contractile activity. However, ovum transport was not completely inhibited. This supports evidence that once the ovum has passed into the isthmic portion, ciliary activity becomes more important than changes in intraluminal pressures when considering the mechanisms of transporting the ovum medially toward the uterine cavity. This is in contrast with the ampullar capture of ova expelled from the ovary. The ampullar activity appears to be more dependent on changes in intraluminal pressures caused by contractile activity for the successful capture of ova.

DISCUSSION

We investigated the physiologic roles of the fallopian tubes and their various parts, including the capture of the ova as they are expelled by the ovaries, together with the accompanying follicular fluid and its various constituents. Once captured by the tubal fimbria, the ova are transported by ciliary activity to the area where they are best fertilized. The tubal environment is also involved in the capacitation of the spermatozoa and ease transport of the sperm to the area where they will fertilize the ova. The tubes also provide an environment conducive to the fertilization and development of the early zygote. The tubal activity is involved in the transport of the zygote medially to aid it in arriving in the uterine cavity, where nidation and further development occur in normal pregnancies.

These various activities occur at definite areas of the tube which can be anatomically designated as the fimbrial tubal structures being involved in the capture of the expelled ova and follicular fluid. The ampullar structures merge with the isthmic portion or the AIJ. It is believed that the ampullar portion distal to the AIJ is where fertilization best occurs, distal to the isthmic portion of the tube is the IUJ. The various portions of the tube appear to have specific and separate functions. It has been demonstrated that rabbits ovulate roughly 10 hr following hCG stimulation (3) and ovulate bilaterally, with up to 10 ova being expelled from each ovary. As this is not a simultaneous event, it requires a given time interval (4). This experiment revealed that the ampullary portion of the tube in rabbits undergoes an increase in tubal activity accompanied by a depression of pressure which syn-

chronizes with the event of ovulation. Although it was not demonstrated by this experiment, the material most likely involved in inducing this enhanced tubal activity appears to be $\text{PGF}_2\alpha$.

These events, including ovulation, fimbrial capture of the ovum, and increased ampullary activity, all suggest the importance of a series of mechanisms participating in the transport of the ovum to the site of fertilization. We found enhanced tubal contractile activity in the tube near ovulation, as evidenced by changes in intraluminal pressures, and showed that inhibiting this contractile activity effectively inhibits ovum capture.

A rapid increase in $\text{PGF}_2\alpha$ in the follicular fluid prior to ovulation has been reported in rats (5) and rabbits (6). In rabbits, it has been reported that follicular preovulatory $\text{PGF}_2\alpha$ levels 60 times baseline concentrations can be attained following hCG administration (7). Expelling the ovum together with follicular fluids is accomplished by the contractions of smooth muscle fibers in the follicular wall (8). Rabbit granulosa cells have been reported to synthesize and secrete $\text{PGF}_2\alpha$ (9). It may be assumed that this increase in $\text{PGF}_2\alpha$ prior to ovulation in the follicular fluid is a requisite to induce contractions of the follicular wall, which then rupture, expelling the ovum and accompanying follicular fluid containing high levels of $\text{PGF}_2\alpha$ into the tubal ampulla (10). It is believed that these elevated levels of $\text{PGF}_2\alpha$ in the follicular fluid are necessary to enhance ovum capture by the tubal fimbria. Indomethacin, which is known as an inhibitor of PG synthesis, inhibits ovulation (11). The ampullary contractions observed following ovulation were likely to have been caused by the influx of high concentrations of $\text{PGF}_2\alpha$, expelled together with the follicular fluid, and inducing smooth muscle contractions of the tubal ampulla.

Once captured by the fimbria, the ovum is said to be transported within a few minutes to the medial ampulla, the region of the AIJ, where it remains for 20–30 hr, waiting to be fertilized by sperm cells traveling distally in the tube (12). In rabbits, isthmic contractility following hCG administration reveals an increase in contractile activity which attains maximal levels at 12–36 hr postadministration. This time period corresponds closely to the interval during which the ovum is retained in the ampulla near the AIJ (13). The AIJ is said to delay the transport of the ovum medially and, in effect, acts as a controlling mechanism for the transport of the fertilized ovum toward the uterine lumen.

Tubal contractility is under the control of the sympathetic nervous system (14,15). The distribution of sympathetic nerve elements is in the inner layer of the annular smooth muscle tissue and is found in increased abundance at the AIJ and UIJ portions of the tubal isthmus (16,17). The outer linear layer and inner annular layer of the tube's smooth muscles contain both α and β receptors, the sensitivity of which is affected cyclically by the influence of endocrine substances. When the α receptors are stimulated, there is an increase in contractility, and when the β receptors are stimulated, there is an inhibition of contractility. These receptors are highly responsive to sex steroids (18) and prostaglandins and are intimately involved in controlling the rhythmic tubal contractions and relaxations necessary for ovum transport (19–22). In rabbits, the elevated estrogens at ovulation stimulate the α receptors, increasing tubal contractility, and are involved in retaining the ovum in the ampulla near the AIJ. After ovulation, the elevation in progesterone stimulates the β receptors, causing relaxation of the AIJ, allowing transport of the ovum into the isthmus portion of the tube (23,24).

Eddy (25) reports that in rabbits, estrogen administration postovulation results in the retention of the ovum near the AIJ. This suggests that estrogen stimulates the α receptors, resulting in increased contractility of the AIJ, which then acts as a limiting sphincter and thus inhibits medial transport of the ova into the isthmus portion of the tube. This was further substantiated by the excision of the AIJ, followed by estrogen, which effectively inhibited medial transport of the ovum in the tubal isthmus. Thus, it is clear that progesterone, which stimulates the β receptors, effecting a smooth muscle relaxation in the tubes, is an indispensable factor in allowing the ovum to be transported from the ampulla into the isthmus portion of the tube.

The tubal ampulla distal to the AIJ has been observed to be the optimal site for fertilization. The ova captured by the fimbrial portion are rapidly transported to a location near the AIJ. This process is said to occur in just a few minutes (26,27). This rapid transport of the ova within the ampullary portion is dependent on ciliary activity and tubal smooth muscle contractions. Halbert *et al.* (28) have reported that, in the rabbit, the ova are transported in the ampulla at a rate of 0.1 mm/min and that isoproterenol, a β stimulant smooth muscle relaxant, has no effect on slowing this rate, emphasizing the importance of ciliary activity in the transport of ova in the ampullary portion of the tube. These ampullary contractions are probably intimately involved in the transport of the ova toward

the uterine cavity, during which time the ova may be fertilized. Thus, we feel that the high concentrations of $\text{PGF}_2\alpha$ observed in the follicular fluid are highly important in inducing transport of the ova from the follicle to the ampulla, then through the tube, until they finally arrive at the uterine cavity for nidation and further development.

CONCLUSIONS

In conclusion, our data based on telemetry received signals revealed that rabbits injected with hCG respond by ovulating at 9.5 ± 1.6 hr postinjection, as evidenced by a sharp drop in tubal pressure, followed by a recovery to twice the control levels, with a disparity in intratubal pressures between contractions and relaxations roughly three times those seen under control conditions.

In intact rabbit fallopian tubes, $\text{PGF}_2\alpha$ and Atonin-O both cause an increase in tubal contractile activity which is effectively inhibited by Utererin. Utererin effectively inhibits tubal contractile activity as demonstrated by a failure to capture ova expelled from the ovaries. However, this inhibitory activity of Utererin can be reversed by the subsequent administration of $\text{PGF}_2\alpha$, which restimulates the tubal tissues to commence contractile activity, and thus allow the fimbrial portions of the tubal ampullae actively to capture ova. Once the ova are captured, Utererin has an inhibitory influence on ovum transport but is unable to halt this process completely, indicating that once the ovum is captured, ciliary activity is more important than tubal contractility in transporting the ova toward the uterine cavity.

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