BIOLOGY OF REPRODUCTION 36, 203–210 (1987)

Sperm Transport and Motility in the Mouse Oviduct: Observations In Situ[1]

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ABSTRACT

Sperm transport and motility were studied through the transparent walls of the mouse oviduct by direct microscopic observation and videomicrography. Observations were made on excised female tracts 1–2 h post-coitus (pc) and 1–2 h before and after the approximate time of ovulation. Motile sperm were seen at the uterine entrance to the uterotubal junction (UTJ) in all females at 1–2 h pc, but in fewer females at later times. The intramural UTJ was usually constricted and held few sperm. The extramural UTJ and adjacent lower isthmus contained many motile sperm at 1–2 h pc. Apparently, the column of sperm moved upwards because in some females, sperm were found in the upper isthmus and not in the UTJ at the later time points. Few sperm were seen in the ampulla in the periovulatory period, and none at 1–2 h pc. There appeared to be two mechanisms retaining sperm in the lower oviduct: immobilization and adherence to the epithelium. Columns of immotile sperm were seen in the lower isthmus of some females. Motile sperm usually appeared to adhere by their heads to the oviductal epithelium, only occasionally breaking free to move vigorously about the lumen.

INTRODUCTION

Movement of sperm through the female tract to the site of fertilization has been investigated mainly by indirect techniques, such as fixing and sectioning the tract (Reinius, 1968; Oura et al., 1970; Olds, 1970; Zamboni, 1972; Chakraborty and Nelson, 1975; Tessler and Olds-Clarke, 1981) or flushing out the luminal contents of the unfixed tract shortly after killing the female (Overstreet and Cooper, 1978, Overstreet et al., 1978; Cummins, 1982; Cummins and Yanagimachi, 1982; Suarez et al., 1983) at various times after mating. The problem with the former method is that the motility of the sperm cannot be evaluated. Motile sperm can be recovered by flushing, but then the site from which they were removed cannot be precisely determined. Moreover, the interaction of the sperm with the tract epithelium cannot be observed. Improved microscopic optics and videomicrographic equipment now make it possible to study sperm *in situ*. Katz and Yanagimachi (1980) used high-speed cinemicrography to study the movement of hamster spermatozoa within the ampulla of the oviduct after the time of fertilization. They were unable to film other sections of the hamster oviduct because it lacked sufficient transparency to permit observation. The mouse, however, possesses a highly transparent oviduct. For this reason, the mouse was used to study sperm transport and motile behavior within the female tract, from the entrance to the uterotubal junction (UTJ) in the uterine lumen to the ostium of the ampulla. Shuttered high-speed videomicrography was used to supplement direct observation as well as allow observation of movements in slow motion.

MATERIALS AND METHODS

Medium

The medium used for bathing the female reproductive tracts had the following composition: 110 mM NaCl, 2.68 mM KCl, 0.36 mM NaH_2PO_4, 25.0 mM $NaHCO_3$, 25.0 mM HEPES (N-2-hydroxyethylpiperazine-N′-2-ethanesulfonic acid), 2.4 mM $CaCl_2$, 0.49 mM $MgCl_2$, 5.56 mM glucose, 1.0 mM pyruvate, 0.006% Na penicillin G, pH 7.6. All organics were purchased from Sigma Chemical Co., St. Louis, MO. The medium was sterilized by filtration through a Millex-GV 0.22-μm filter and kept frozen in aliquots.

Accepted July 15, 1986.
Received April 21, 1986.
[1] This work was supported by NIH Research Grant HD19584.
[2] Reprint requests.

Video Equipment

The sperm were videotaped at a rate of 60 fields per s in 1/500 s exposures by a Tritronics shuttered high-speed video camera (Burbank, CA). A record of elapsed time in 0.01-s intervals, generated by a For A video time generator (model VTG 33, Los Angeles, CA), was simultaneously recorded on a JVC3/4-inch (2.6-cm) U-matic video cassette recorder (model CR06600U, Victor Co. of Japan).

Preparation of Female Reproductive Tracts

Adult outbred Swiss mice obtained from Charles River (Kingston, NY) were maintained on a 14L:10D cycle, with lights off at 0930. Males were housed individually. Two virgin females were placed into the cage of each male at 0930 h, which would be the time of the onset of estrus in females entering Day 1 of their 4- to 5-day cycle (Hafez, 1970). A total of 6–8 females were placed with males each day to ensure that at least one would be entering the estrous phase. They were then checked hourly until 1330 h for vaginal plugs. Whenever mating occurred, unmated females were removed. The mated female was left with the male for 1 h (=1–2 h postcoitus [pc]) or until 1730 h or 1930 h. These two time points were approximately 1 h before and 1 h after ovulation, as determined during pilot experiments. At the appropriate time, the female was killed by CO_2 inhalation and placed immediately in a 37°C chamber. Each oviduct, along with the ovary and uterine horn, was removed. The ovaries were carefully cut away and the uterine horns were trimmed down to 5 mm. The preparations were rinsed with 37°C medium, placed on slides prewarmed to 37°C, covered with medium, and capped by a coverslip supported by 10:1 vaseline-paraffin mixture. One slide was placed on a microscope stage kept at 37°C by an Arenberg Sage Air Curtain (model 279, Boston, MA), while the other was stored in the dark in a humidified incubator. The activity of sperm within the uterine and oviductal lumena was observed directly through Zeiss differential interference contrast optics and videotaped for additional observations at real time and in slow motion. Each slide was observed and videotaped for about 10 min. The location of the sperm within the tract was first determined at 100 × magnification; the magnification was then increased to 400 × to study the motility of the sperm and their interaction with the epithelial walls.

Regions of the oviduct were those defined by Nilsson and Reinius (1969), with the additional division of the isthmus into lower (proximal to the uterus) and upper segments.

Three criteria were used to determine that the sperm being studied were in a normal physiological environment: 1) sperm escaping from the cut end of the uterus were motile, 2) cilia of ampullar epithelial cells were actively beating, and 3) artifactual contractions did not occur during the observation period. Artifactual contractions are those that occur in direct response to manipulation of the tract.

RESULTS

Females were placed with males at 0930 h, which was the onset of darkness and estrus for those females in the first day of their estrous cycle. Of 34 matings, 1 occurred between 0930 h and 1030 h, 4 between 1030 h and 1130 h, 18 between 1130 h and 1230 h, and 11 between 1230 h and 1330 h. The mode of 1130 h to 1230 h was 5–7 h before ovulation, based on observations of females killed at various times before 1930 h. The oviducts of 7 females were examined at each time point, i.e. 1–2 h pc, 1730 h, and 1930 h.

The transparency of the mouse female reproductive tract is apparent in Figure 1. The colliculus tubarius (CT) can be seen through the uterine wall. When the ovaries were removed, a more shallow slide preparation

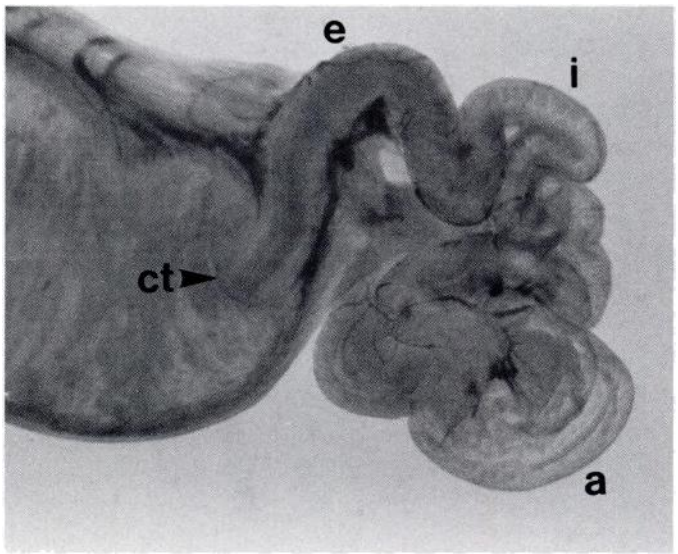

FIG. 1. The preparation of mouse oviduct used for observing sperm in situ: colliculus tubarius (*ct*, visible through the uterine wall), the extramural segment of the uterotubal junction (*e*), the isthmus (*i*), and the ampulla (*a*). Brightfield illumination, × 20.

could be made, illuminating more of the isthmic lumen. Not all sections of the female reproductive tract were positioned in each preparation so that their luminal contents could be seen. Nevertheless, if a section was not visible, the tract was not manipulated because this would stimulate waves of contraction that were observed at times to displace luminal contents, including sperm. Observations were simply made wherever possible in each tract preparation. When something is reported to have been observed in a female, the observation was made in one or both sides of the tract.

The regions of the tract resembled those described by Nilsson and Reinius (1969), which were based on light and electron micrographs. That paper should be consulted for more detailed descriptions of oviductal histology. The observations described below of sperm distribution within the tract are summarized in Table 1.

Uterotubal Junction (UTJ)

The entrance to the UTJ could be seen at the tip of the CT, which protrudes into the uterine lumen (Fig. 1). Sperm were present in the uterine lumen at the CT in 6/6 females at 1–2 h pc. At 1730 h, sperm were observed at the CT in only 4/6 females and at 1930 h in only 1/5 females. The heads of many sperm appeared to adhere by the rostral tip to the surface of the CT or the uterine wall. Sperm occasionally swam away from either surface, so this apparent adherence was not irreversible. The site of adherence was the acrosomal ridge, the most rostral point on the head. The movement of the sperm in the uterus was somewhat sinuous, while sperm escaping from the open end of the uterus moved more rapidly, either in linear or circular trajectories. The uterine fluid appeared to be viscous, which might account for the more rapid movement of sperm when diluted in medium. Eventually most of the escaped sperm adhered to the slide or to blood cells by the acrosomal ridge.

The wall of the UTJ was thicker than the other oviductal walls. The lumen was also the most simple: apparently there were only shallow longitudinal invaginations in the epithelial wall (Fig. 2A).

The lumen of the intramural segment of the UTJ could only be seen in 4/7 females at 1–2 h pc. Sperm were only found in the lumen, distal to the CT, of two of those mice. Apparently, the lumina were constricted, making their detection difficult and excluding sperm. Even the lumen in which sperm were detected had a relatively small diameter. The lumina appeared to be constricted or narrow at later time points as well. Sperm were detected in the intramural segment of 3/6 females at 1730 h and 3/5 females at 1930 h, but they were not numerous and the lumen surrounding them was completely closed.

In contrast, many motile sperm were observed in the extramural segment of the UTJ in 6/7 females at 1–2 h pc and 5/6 females at 1730 h. Most of the sperm appeared to adhere to the epithelial walls, but a few were observed to break away and dart actively about the lumen. By 1930 h, sperm were seen in this segment in only 3/7 females.

Isthmus

The isthmic portion of the oviduct could be identified by epithelial cell inclusions, which are highly refractile spheres 1–10 μm in diameter. The walls of the isthmus were thinner than those of the UTJ and contained invaginations or folds that were more circularly oriented (Fig. 2B).

The lower isthmus (LI, the portion proximal to the uterus) contained the majority of the sperm at all time points. Motile sperm were present in 7/7 females at 1–2 h pc, 7/7 females at 1730 h, and 7/7 females at 1930 h. Sperm were distributed in folds as well as in the central portion of the lumen. The heads also appeared to adhere to the epithelium by the convex surface of the rostral half of the head. The adherent heads of the sperm in inpocketings were usually attached to the base of the fold (Fig. 3). The widths of the central lumen and inpocketings were less than the lengths of the sperm (approximately 120 μm); therefore, movement of sperm in those spaces was

TABLE 1. A summary of the location of sperm in the mouse reproductive tract at 1–2 h pc, 1730 h (approximately 1–2 h before ovulation), and 1930 h (approximately 1–2 h after ovulation).

Section	1–2 h postcoitus	1730 h	1930 h
Colliculus tubarius	6/6	4/6	1/5
Intramural UTJ	2/4	3/6	3/5
Extramural UTJ	6/7	5/6	3/7
Lower isthmus	7/7	7/7	7/7
Upper isthmus	0/6	4/7	4/6
Ampulla	0/7	2/6	2/7

*Seven females were used for each time point. Since the lumena of all sections of the tract were not visible in every female, the numerator indicates the number of females in which sperm were present and the denominator indicates the number of females in which that particular segment was in a favorable position for observation.

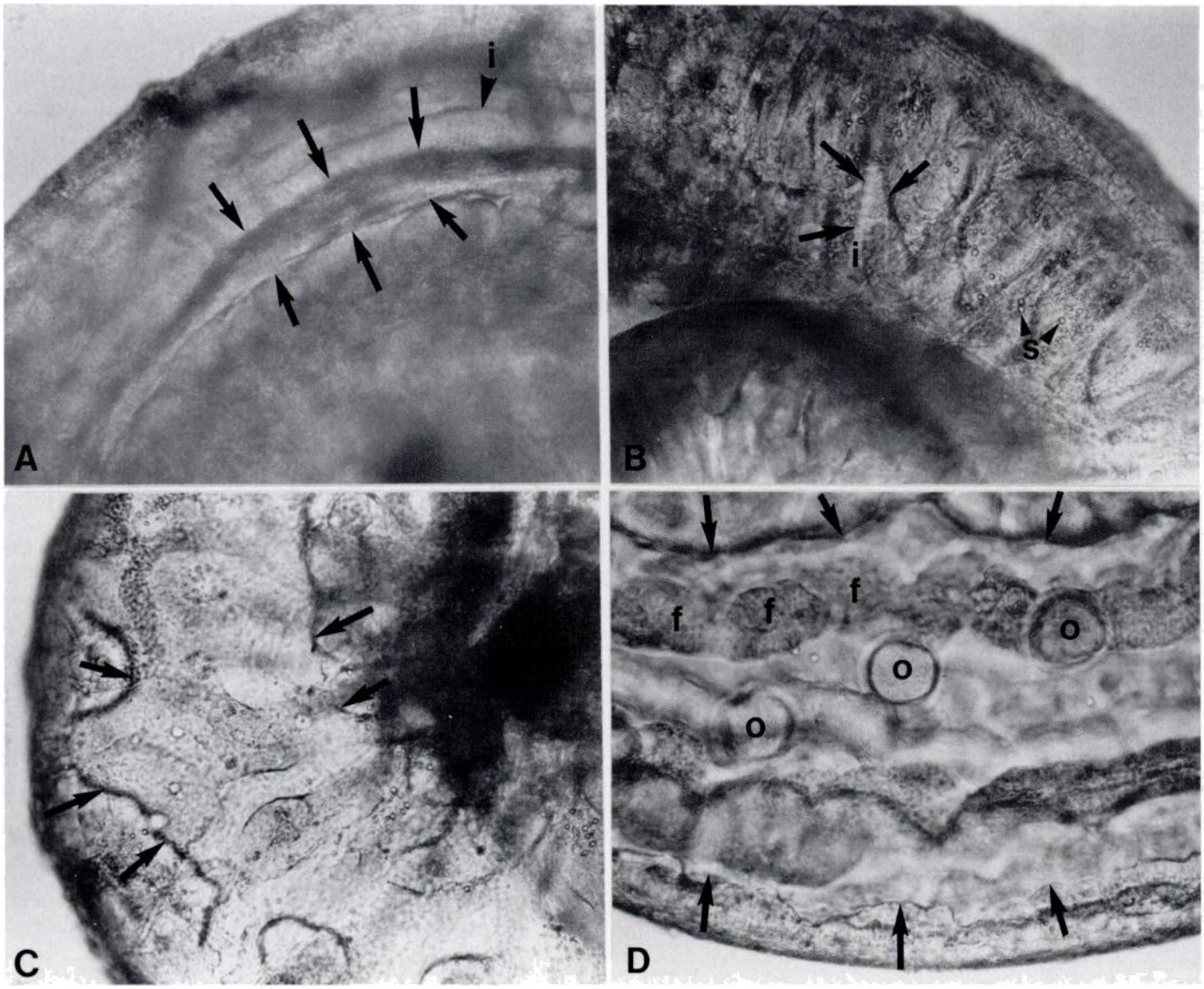

FIG. 2. Four segments of the mouse oviduct (brightfield, X 136. The lumina are indicated by *arrows*. *A*) The extramural segment of the uterotubal junction. The wall is thicker and the lumen more simple here than in more distal segments of the oviduct. A longitudinally oriented invagination (*i*) is indicated. *B*) The isthmus. Note the refractile spherical inclusions (*s*) in the epithelium and the peripherally directed inpocketings (*i*) of the epithelial wall. *C*) The ampullary-isthmic junction. Note the irregularly shaped lumen, intermediate in appearance between those of the isthmus and ampulla. *D*) The ampulla. The epithelium has longitudinal, instead of circular, folds (*f*). Three oocytes (*o*) surrounded by zonae pellucidae but not cumulus cells are visible within the lumen. These oocytes are shown for size because they are more clearly visible than freshly ovulated oocytes in cumulus. When present, the cumulus nearly spans the width of the lumen.

rather restricted. At times, the sperm would break free of their attachment to the epithelium and move vigorously about the lumen. Although the lumen was generally too small to allow determination of the type of motility, at least some sperm appeared to be hyperactivated.

In 2/7 females at 1–2 h pc, 4/7 at 1730 h, and 2/7 at 1930 h, a segment of the LI lumen was filled with immotile sperm. There was a short intermediate zone extending 100–300 μm along the lumen, which contained immotile sperm and slow, sinuously moving sperm, then a zone of vigorously motile sperm. Motile sperm were seen on both sides of the segment when both sides were visible.

The upper isthmus (UI) was identical to the LI in appearance and was only identified by its proximity to the ampulla. No sperm were ever observed in the UI at 1–2 h pc (0/6). Sperm were present in the upper half of the isthmus at the later time points (4/7 females at 1530 h and 4/6 females at 1930 h), but in

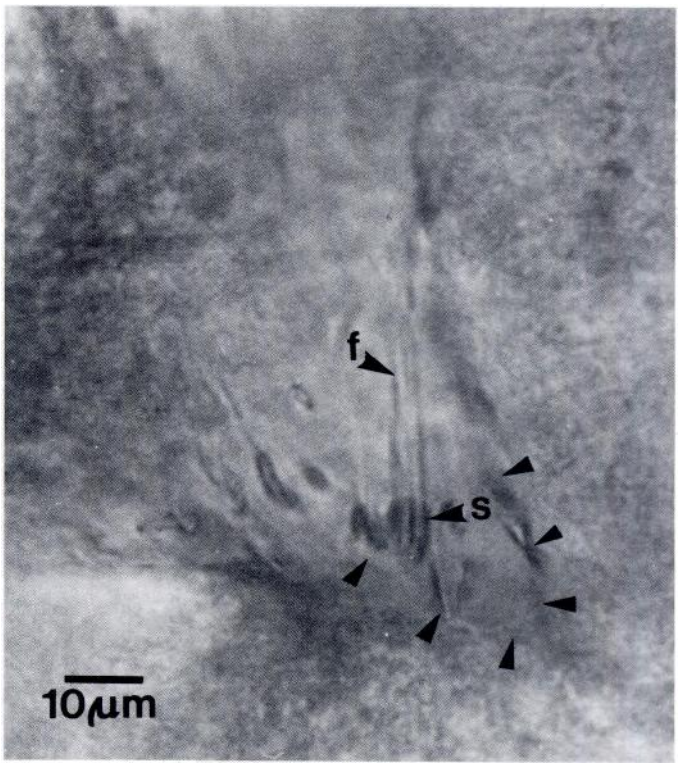

FIG. 3. Living sperm within a luminal pocket of the isthmus. The sperm heads (*s*) are adhering to the epithelial wall (*arrows*). The flagella (*f*) were beating when photographed and therefore do not show clearly.

much lower numbers than in the LI. In only one case were sperm observed in the UI near oocytes in the ampulla. These few sperm appeared hyperactivated and adhered only intermittently to the epithelium.

Globules ranging in size up to about 10 μm in diameter were seen in the lumen of the entire isthmus at all time points (Fig. 4). They also appeared in the lumen of the extramural UTJ of 3/7 females at 1–2 h pc and 4/6 females at 1730 h. At 1930 h, they appeared in 3/6 females and only when sperm were also visible.

Ampulla

The ampullary-isthmic junction was intermediate in appearance between the isthmus and the ampulla in that its wall had both longitudinal and circular folds and was intermediate in thickness (Fig. 2C). Sperm were never observed in its lumen.

The ampulla was by far the most transparent portion of the oviduct (Fig. 2D). The lumen was wider in places than the length of mouse sperm, so that this was the least restrictive compartment of the oviduct. The epithelium tended to fold longitudinally, although knobs of epithelial wall also projected into the lumen. Cells with motile cilia were scattered about the lumen. They were more frequent proximal to the ovary in the preampulla.

No sperm were observed in the ampullae or preampullae of females at 1–2 h pc. Three or fewer hyperactivated sperm were seen in the ampullae of 2/6 females at 1730 h, and in 2/7 females at 1930 h, 1 of which was in the perivitelline space of an oocyte at 1930 h. Eggs could be seen through the ampullar wall in 2/7 females at 1730 h and 5/7 females at 1930 h. Globules were never seen in the ampulla, except when they were observed entering the lumen during artifactually induced contractions.

DISCUSSION

These results provide confirmation of conclusions drawn from less direct methods of studying sperm transport and add new observations on the oviductal environment and the behavior of sperm within the lumen.

Motile sperm were observed outside the CT in all females at 1–2 h pc and in about half of the females before ovulation. They were present regardless of whether the intramural segment of the UTJ appeared to be constricted. It is conceivable that these sperm could enter the oviduct, especially when the intramural UTJ was not constricted, but it seems unlikely that they would fertilize oocytes, since many more

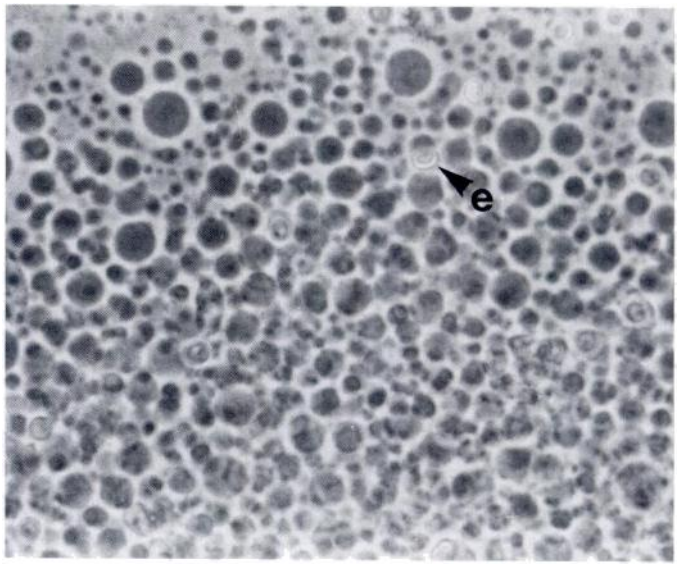

FIG. 4. Contents of the lumen of the lower isthmus, extruded after cutting the isthmus into sections. The *dark spheres* are isthmic globules. An erythrocyte (*e*) is indicated for scale. Phase contrast, X 530.

motile sperm were situated between them and the ovary. Experiments with ligation of the UTJ in the rabbit (Harper, 1973) and the pig (Hunter, 1984) indicate that the fertilizing sperm derived from an oviductal population established within a few hours of mating. The observed constriction of the intramural UTJ is in agreement with results obtained by perfusion fixation of mouse oviducts (Oura et al., 1970; Zamboni, 1972). In those studies, it was observed that the lumen of the intramural UTJ was patent immediately after copulation; but, at some time after 1 h pc, it became constricted by muscular contraction and the elongation of microvilli.

The distribution of sperm within the oviduct was found to be similar to that reported for mice by others who counted the numbers of sperm present in fixed and embedded sections of oviduct. The general finding was that the majority of oviductal sperm were located in the portion of the oviduct closest to the UTJ before and shortly after ovulation (Olds, 1970; Zamboni, 1972; Nicol and McLaren, 1974; Tessler and Olds-Clarke, 1981). In this study, numerous sperm were found in both the extramural UTJ and lower isthmus at 1–2 h pc and before the approximate time of ovulation, but sperm were not seen in the extramural UTJ in half of the females after the approximate time of ovulation. It could not be determined whether sperm were lost from this area by phagocytosis or transport. Phagocytotic loss is possible because Chakraborty and Nelson (1975) found mouse sperm in phagocytic vacuoles in the epithelium of caudal loops of the "extramural portion of the isthmus" 15–22 h pc. Transport is also likely, because groups of sperm were found in the upper isthmus only at the later time points. The column of sperm in the lower oviduct could have been transported upward by contractions of the oviduct. Battalia and Yanagimachi (1979) found that oviductal contractions moved isthmic luminal contents towards the ampulla during the periovulatory period in the hamster. In this study, oviductal contractions stimulated by manipulation of the oviduct were seen to dislodge some of the sperm and to transport globules into the ampulla. If the sperm were transported by their own flagellar motion, it would have been a gradual process because most sperm appeared to adhere to the oviductal wall, rarely breaking away to move any distance.

As in this study, few sperm have ever been found in sections of the mouse ampulla. Stefanini et al. (1969) only found sperm in the ampulla that were not associated with oocytes after the majority of oocytes had been penetrated. They also found penetration of all oocytes to take 2–2.5 h from the time of penetration of the first oocyte, which indicates that sperm arrive gradually at the site of fertilization. Tessler and Olds-Clarke (1981) reported very low numbers of sperm associated with egg clumps removed from the oviduct. Both authors concluded that the first sperm to reach the eggs are probably the ones that fertilize. In this study, the few sperm observed in the ampulla moved actively about in the lumen in such a manner that would surely lead to contract with an egg mass if it were present. Katz and Yanagimachi (1980) observed similar behavior of hamster sperm in the ampullar lumen 4 h after the expected time of fertilization. They used this time point because they were unable to find sufficient numbers of sperm for motility analysis in the ampulla at the expected time of fertilization. Low numbers of sperm have also been found at the site and time of fertilization by flushing the oviducts of hamsters (Cummins and Yanagimachi, 1982) and rabbits (Overstreet and Cooper, 1978).

Two possible mechanisms for retaining sperm in the lower segments of the oviduct were apparent in this study: immobilization of sperm in the lower isthmus and adherence of sperm to the epithelial walls. In the rabbit, nearly immotile sperm were flushed from the isthmus (Overstreet and Cooper, 1975; Cooper et al., 1979). The sperm became motile if diluted and incubated in media or ampullar fluid (Overstreet et al., 1980), implicating a molecular motility inhibitor. The present work is the first report of immotile sperm being observed in a mammal *in situ*. An inhibitor may also be implicated in the suppression of mouse sperm motility, because a recovery zone could be seen between the motile and immotile sperm. In the case of the mouse, the mechanism must be very limited spatially, because only short segments of the isthmus held immotile sperm; therefore, if a molecular inhibitor is involved, it must be either unstable or ineffective at low concentration. A molecule that supresses motility by increasing the viscoelasticity of the medium meets the latter requirement. Such a molecule has been implicated in the immobilization of rat sperm in the caudal epididymis (Usselman and Cone, 1983). On the other hand, a molecule that supports motility, such as an energy

source, could be lacking in that area of the lumen because of local inhibition of epithelial secretion or localized depletion by excessive numbers of sperm. Localized constriction of the oviductal wall could mechanically immobilize sperm and remove adequate amounts of substances required for motility. Nilsson and Reinius (1969) reported localized constriction of the isthmic lumen in the mouse.

Because sperm immobilization is less prevalent in the mouse than in the rabbit, adherence of the sperm to the oviductal walls may play a more significant role in isthmic retention of mouse sperm. The observed adhesion was weak enough to allow sperm to break away periodically and move within the lumen before reestablishing contact with the epithelium. Sperm did not adhere to the ampullar epithelium. Either the walls of the ampulla lacked receptors or sufficiently charged surfaces, or the sperm lost cell surface receptors or charge during capacitation. Cell surface changes occurring during capacitation in vivo are well documented for sperm (see review by Yanagimachi, 1981). Regardless of the mechanism involved, this phenomenon can account for the gradual movement of sperm into the ampulla.

Globules resembling vesicles were observed in the lumen of the isthmus and the extramural segment of the UTJ. Globules of similar appearance were recovered in flushings from the ampullae of mated rabbits (Suarez et al., 1983). They are not apparent in previously published micrographs of mouse oviducts rapidly fixed by vascular perfusion (Zamboni, 1972; Chakraborty and Nelson, 1975) to the extent that they were observed during this study. Globules resulting from apocrine secretion have been reported in humans and macaques (Jansen, 1984). Upon acquisition of a new, more light-sensitive video camera (Cohu 5372-2020, Carson Optical, Oakland, CA), these experiments with mice were repeated. In the repeated experiments, sperm behavior was not different, including immobilization in segments of the lower isthmus. In place of globules in the lumina, however, blebs were seen on the epithelial surfaces. Globules could be induced to form by pressing heavily on the coverslip, inducing contractions of the musculature, or observing the preparations through the microscope for more than 10 min. Apparently, the globules observed initially had been artifactually induced, probably by the strong light (or accompanying heat) required by the shuttered videocamera. It is also possible that the globules observed in rabbits were created by forcing fluid through the oviduct; in humans, by tissue trauma induced by immersion fixation; and in macaques by trauma arising from the lengthy dissection that preceeded perfusion (see Jansen and Bajpai, 1983). Nevertheless, the blebbing of oviductal epithelium and the ability of the luminal surface of the plasma membrane to form vesicles are noteworthy characteristics that may be the result of membrane components that serve a special function.

In conclusion, these studies have confirmed deductions about storage of sperm in the lower isthmus and of low sperm:egg ratios in the ampulla at fertilization that were drawn mainly from indirect methods. They have also provided information about the behavior of sperm within the oviduct.

ACKNOWLEDGMENTS

I am indebted to Dr. Irwin Liu for his generous donation of laboratory space and equipment. I would also like to thank Richard Osman and Dr. Stanley Meizel for critical evaluation of the manuscript, Dr. Allen Enders and Sandy Enders for consultation on the luminal globules, and Robert Munn for producing high-quality prints.

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