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Transportation of sperm

Site of semen deposition

The site of semen deposition is not easy to establish in many species because it must be determined by examining the female immediately after coitus and by considering the anatomy of the penis, vagina and cervix during coitus. However, it has been accomplished for humans, in which semen has been observed pooled in the anterior vagina near the cervical os shortly after coitus. Within minutes of vaginal deposition, human sperm begin to leave the seminal pool and swim into the cervical canal .

Vaginal defenses against infectious organisms may affect sperm

The vagina is open to the exterior and thus to infection, especially at the time of coitus; therefore, it is well equipped with antimicrobial defenses. These defenses include acidic pH and immunological responses and can damage sperm as well as infectious organisms. To enable fertilization to take place, both the female and the male have adopted mechanisms for protecting sperm. In humans, semen is deposited at the external os of the cervix so that sperm can quickly move out of the vagina. Human sperm must contend, however briefly, with the acidic pH of vaginal fluid. The vaginal pH of women is normally five or lower, which is microbicidal for many sexually transmitted disease pathogens. Evidence indicates that the acidity is maintained through lactic acid production by anaerobic lactobacilli that feed on glycogen present in shed vaginal epithelial cells. Lowering pH with lactic acid has been demonstrated to immobilize bull sperm . The pH of seminal plasma ranges from 6.7 to 7.4 in common domestic species (Roberts, 1986) and has the potential to neutralize vaginal acid. Vaginal pH was measured by radio-telemetry in a fertile human couple during coitus. The pH rose from 4.3 to 7.2 within 8 s of the arrival of semen; whereas, no change was detected when the partner used a condom Males may also overcome female defenses by inseminating many sperm.

Sperm transport through the cervix

In some species, the cervical canal widens under the influence of estrogen. Fluoroscopy and scintigraphy have been used in domestic dogs and cats to examine cervical patency. Opening of the cervix in these species has been correlated with estrus. Radioopaque fluid and also human serum albumin radiolabelled with technetium 99 could be seen rapidly passing through the cervix and filling the uterine

lumen after deposition in the cranial vagina at estrus. Cervical mucus presents a greater barrier to abnormal sperm that cannot swim properly or that present a poor hydrodynamic profile than it does to morphologically normal, vigorously motile sperm and is thus thought as one means of sperm selection

Sperm transport through the uterus

At only a few centimetres in length, the human uterine cavity is relatively small and could be traversed in less than 10 min by sperm swimming at about 5 mm/min, which is the swimming speed of sperm in aqueous medium (Mortimer and Swan, 1995). The actual rate of passage of human sperm through the uterus is difficult to determine due to experimental limitations.

Transport of sperm through the uterus is likely aided by pro-ovarian contractions of the myometrium. Ultrasonography of the human uterus has revealed cranially directed waves of uterine smooth muscle contractions that increase in intensity during the late follicular phase. In humans, contractile activity of uterine muscle may draw sperm and watery midcycle mucus from the cervix into the uterus.

Transport through the uterotubal junction

The uterotubal junction presents anatomical, physiological and/or mucous barriers to sperm passage in most mammals. Anatomically, the lumen in species as distantly related as dairy cattle and mice is particularly tortuous and narrow

The narrowness of the lumen is especially apparent in living tissue and in frozen sections, in which tissue does not shrink as it does during standard preparation of paraffin-embedded sections. Within the lumen of the junction, there are large and small folds in the mucosa

Rapid sperm transport

Sperm have been recovered in the cranial reaches of the tubal ampulla only minutes after mating or insemination in humans and several other species of mammals. Rapid transport of sperm into the Fallopian tube would seem to counter the proposed model of sperm swimming one-by-one through the uterotubal junction. Motile sperm gradually pass through the uterotubal junction to establish a tubal population capable of fertilizing. The contractions may serve primarily to draw sperm into the cervix but result in overshooting of some sperm. As described above, motile human sperm have been recovered from Fallopian tubes within an hour of insemination; however, it is not known whether function was normal in these women.

A sperm reservoir in the Fallopian tube

As sperm pass through the uterotubal junction and enter the tubal isthmus, they may be trapped and held in a reservoir. Yanagimachi and Chang (1963) were first to describe a reservoir of sperm in the hamster tubal isthmus. Since then, evidence has been found for the formation of sperm storage reservoirs in a variety of species

The Fallopian tube provides a haven for sperm. Unlike the vagina, cervix and uterus, the tube does not respond to insemination with an influx of leukocytes.

In addition to providing a haven, the storage reservoir maintains the fertility of sperm until ovulation. *In vitro*, sperm fertility and motility are maintained longer when sperm are incubated with endosalpingeal epithelium. Entrapment and storage of sperm in the initial segment of the tube may serve to prevent polyspermic fertilization by allowing only a few sperm at a time to reach the oocyte in the ampulla.

Advancement of sperm beyond the tubal reservoir

Theoretically, sperm could be released from the reservoir either through loss of binding sites on the epithelium or by alterations in the sperm themselves. Changes in the hormonal state of endosalpingeal epithelium related to impending ovulation do not affect the density of binding sites for sperm in many species and in women relatively equal numbers of sperm bind to endosalpingeal explants recovered at different times of the ovarian cycle. Thus, it appears that the epithelium does not release sperm by reducing binding sites. Instead, current evidence indicates that changes in sperm bring about their release.

Sperm undergo two changes in preparation for fertilization: capacitation and hyperactivation. Capacitation involves changes in the plasma membrane, including shedding of proteins and cholesterol, that prepare sperm to undergo the acrosome reaction and fertilize oocytes (reviewed by De Jonge, 2005) and therefore loss or modification of proteins on the surface of the plasma could reduce affinity for the endosalpingeal epithelium. Hyperactivation, on the other hand, is a change in flagellar beating that typically involves an increase in the flagellar bend amplitude (Figure 1C). This can provide the force necessary for overcoming the attraction between sperm and epithelium. Although a distinct tubal sperm reservoir has not been reported for humans, hyperactivation and capacitation could serve to speed sperm movement into the ampulla as the time of ovulation approaches.

Hyperactivation of sperm and the final stages of transport

At some point in the female tract, most likely in the Fallopian tubes, sperm become hyperactivated. In aqueous media *in vitro*, hyperactivated sperm swim vigorously but in circular or erratic patterns. *In vivo*, the physical environment encountered by sperm is quite different and evidence indicates that hyperactivation is required by sperm to progress towards the oocyte and penetrate its vestments. As discussed above, hyperactivation may assist sperm in detaching from the endosalpingeal epithelium. In

addition, hyperactivation enhances the ability of sperm to swim through viscoelastic substances such as mucus in the tubal lumen and the extracellular matrix of the cumulus oophorus. Mucus fills the uterotubal junction and extends into the isthmus in humans. In addition to assisting sperm in reaching the oocyte, hyperactivation also aids sperm in penetrating the zona pellucida. When hyperactivation was blocked in capacitated, acrosome-reacted hamster sperm bound to the zona, they were unable to penetrate it .