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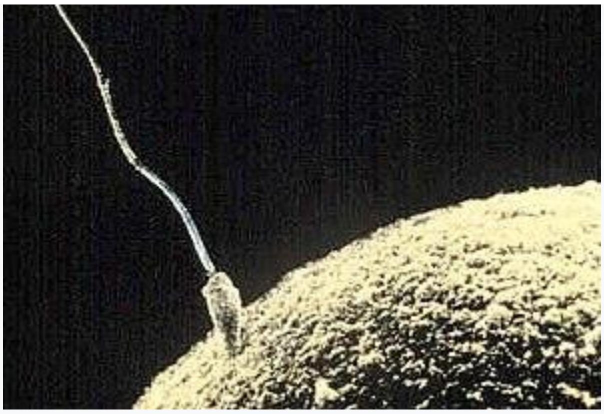
Aula 5. Fertilisation



Sperm and ovum fusing

Fertilisation or **fertilization** (see spelling differences), also known as **generative fertilisation**, **syngamy** and **impregnation**,[1] is the fusion of gametes to give rise to a new individual organism or offspring and initiate its development. Processes such as insemination or pollination which happen before the fusion of gametes are also sometimes informally called fertilization.[2] The cycle of fertilisation and development of new individuals is called sexual reproduction. During double fertilisation in angiosperms the haploid male gamete combines with two haploid polar nuclei to form a triploid primary endosperm nucleus by the process of vegetative fertilisation.

History[edit]

In Antiquity, Aristotle conceived the formation of new individuals through fusion of male and female fluids, with form and function emerging gradually, in a mode called by him as epigenetic.[3]

In 1784, Spallanzani established the need of interaction between the female's ovum and male's sperm to form a zygote in frogs.[4] In 1827, von Baer observed a therian mammalian egg for the first time.[3] Oscar Hertwig (1876), in Germany, described the fusion of nuclei of spermatozoa and of ova from sea urchin.[4]

Evolution[edit]

The evolution of fertilisation is related to the origin of meiosis, as both are part of sexual reproduction, originated in eukaryotes. There are two conflicting theories on how the couple meiosis–fertilisation arose. One is that it evolved from prokaryotic sex (bacterial recombination) as eukaryotes evolved from prokaryotes.[*citation needed*] The other is that mitosis originated meiosis.[5]

Fertilisation in animals[edit]

The mechanics behind fertilisation has been studied extensively in sea urchins and mice. This research addresses the question of how the sperm and the appropriate egg find each other and the question of how only one sperm gets into the egg and delivers its contents. There are three steps to fertilisation that ensure species-specificity:

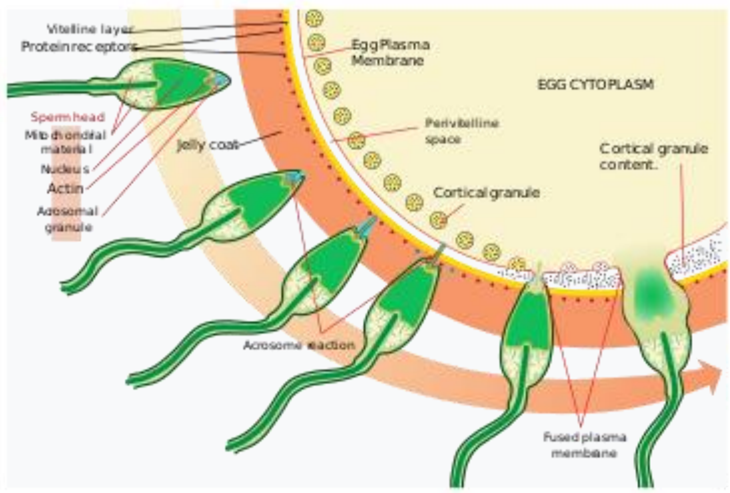
1. Chemotaxis
2. Sperm activation/acrosomal reaction
3. Sperm/egg adhesion

Internal vs. external[edit]

Consideration as to whether an animal (more specifically a vertebrate) uses internal or external fertilisation is often dependent on the method of birth. Oviparous animals laying eggs with thick calcium shells, such as chickens, or thick leathery shells generally reproduce via internal fertilisation so that the sperm fertilises the egg without having to pass through the thick, protective, tertiary layer of the egg. Ovoviviparous and viviparous animals also use internal fertilisation. It is important to note that although some organisms reproduce via amplexus, they may still use internal fertilisation, as with some salamanders. Advantages to internal fertilisation include: minimal waste of gametes; greater chance of individual egg fertilisation, relatively "longer" time period of egg protection, and selective fertilisation; many females have the ability to store sperm for extended periods of time and can fertilise their eggs at their own desire.

Oviparous animals producing eggs with thin tertiary membranes or no membranes at all, on the other hand, use external fertilisation methods. Such animals may be more precisely termed ovuliparous.[19] Advantages to external fertilisation include: minimal contact and transmission of bodily fluids; decreasing the risk of disease transmission, and greater genetic variation (especially during broadcast spawning external fertilisation methods).

Sea urchins[edit]



Acrosome reaction on a sea urchin cell.

Sperm find the eggs via chemotaxis, a type of ligand/receptor interaction. Resact is a 14 amino acid peptide purified from the jelly coat of *A. punctulata* that attracts the migration of sperm.

After finding the egg, the sperm penetrates the jelly coat through a process called sperm activation. In another ligand/receptor interaction, an oligosaccharide component of the egg binds and activates a receptor on the sperm and causes the acrosomal reaction. The acrosomal vesicles of the sperm fuse with the plasma membrane and are released. In this process, molecules bound to the acrosomal vesicle membrane, such as bindin, are exposed on the surface of the sperm. These contents digest the jelly coat and eventually the vitelline membrane. In addition to the release of acrosomal vesicles, there is explosive polymerisation of actin to form a thin spike at the head of the sperm called the acrosomal process.

The sperm binds to the egg through another ligand reaction between receptors on the vitelline membrane. The sperm surface protein bindin, binds to a receptor on the vitelline membrane identified as EBR1.

Fusion of the plasma membranes of the sperm and egg are likely mediated by bindin. At the site of contact, fusion causes the formation of a fertilisation cone.

Mammals[edit]

Mammals internally fertilise through copulation. After a male ejaculates, many sperm move to the upper vagina (via contractions from the vagina) through the cervix and across the length of the uterus to meet the ovum. In cases where fertilisation occurs, the female usually ovulates during a period that extends from hours before copulation to a few days after; therefore, in most mammals it is more common for ejaculation to precede ovulation than vice versa.

When sperm are deposited into the anterior vagina, they are not capable of fertilisation (i.e., non-capacitated) and are characterized by slow linear motility patterns. This motility, combined with muscular contractions enables sperm transport towards the uterus and fallopian tubes.[20] There is a pH gradient within the micro-environment of the female reproductive tract such that the pH near the vaginal opening is lower (approximately 5) than the fallopian tubes (approximately 8).[21] The sperm-specific pH-sensitive calcium transport protein called CatSper increases the sperm cell permeability to calcium as it moves further into the reproductive tract. Intracellular calcium influx contributes to sperm capacitation and hyperactivation, causing a more violent and rapid non-linear motility pattern as sperm approach the oocyte. The capacitated spermatozoon and the oocyte meet and interact in the *ampulla* of the fallopian tube. Rheotaxis, thermotaxis and chemotaxis are known mechanisms that guide sperm towards the egg during the final stage of sperm migration.[22] Spermatozoa respond (see Sperm thermotaxis) to the temperature gradient of ~2 °C between the oviduct and the ampulla,[23] and chemotactic gradients of progesterone have been confirmed as the signal emanating from the cumulus oophorus cells surrounding rabbit and human oocytes.[24] Capacitated and hyperactivated sperm respond to these gradients by changing their behaviour and moving towards the cumulus-oocyte complex. Other chemotactic signals such as formyl Met-Leu-Phe (fMLF) may also guide spermatozoa.[25]

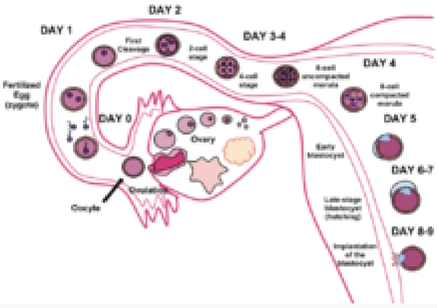
The zona pellucida, a thick layer of extracellular matrix that surrounds the egg and is similar to the role of the vitelline membrane in sea urchins, binds the sperm. Unlike sea urchins, the sperm binds to the egg before the acrosomal reaction. ZP3, a glycoprotein in the zona pellucida, is responsible for egg/sperm adhesion in mice. The receptor galactosyltransferase (GalT) binds to the N-acetylglucosamine residues on the ZP3 and is important for binding with the sperm and activating the acrosome reaction. ZP3 is sufficient though unnecessary for sperm/egg binding. Two additional sperm receptors exist: a 250kD protein that binds to an oviduct secreted protein, and SED1, which independently binds to the zona. After the acrosome reaction, the sperm is believed to remain bound to the zona pellucida through exposed ZP2 receptors. These receptors are unknown in mice but have been identified in guinea pigs.

In mammals, the binding of the spermatozoon to the GalT initiates the acrosome reaction. This process releases the hyaluronidase that digests the matrix of hyaluronic acid in the vestments around the oocyte. Additionally, heparin-like glycosaminoglycans (GAGs) are released near the oocyte that promote the acrosome reaction.[26] Fusion between the oocyte plasma membranes and sperm follows and allows the sperm nucleus, the typical centriole, and atypical centriole that is attached to the flagellum, but not the mitochondria, to enter the oocyte.[27] The protein CD9 likely mediates this fusion in mice (the binding homolog). The egg "activates" itself upon fusing with a single sperm cell and thereby changes its cell membrane to prevent fusion with other sperm. Zinc atoms are released during this activation.[*citation needed*]

This process ultimately leads to the formation of a diploid cell called a zygote. The zygote divides to form a blastocyst and, upon entering the uterus, implants in the endometrium, beginning pregnancy. Embryonic implantation not in the uterine wall results in an ectopic pregnancy that can kill the mother.

In such animals as rabbits, coitus induces ovulation by stimulating the release of the pituitary hormone gonadotropin; this release greatly increases the likelihood of pregnancy.

Humans



Fertilisation in humans. The sperm and ovum unite through fertilisation, creating a zygote that (over the course of 8-9 days) implants in the uterine wall, where it resides for nine months.

Fertilisation in humans is the union of a human egg and sperm, usually occurring in the ampulla of the fallopian tube, producing a zygote cell, or fertilised egg, initiating prenatal development. Scientists discovered the dynamics of human fertilisation in the nineteenth century.

The term *conception* commonly refers to "the process of becoming pregnant involving fertilization or implantation or both".[28] Its use makes it a subject of semantic arguments about the beginning of pregnancy, typically in the context of the abortion debate. Upon gastrulation, which occurs around 16 days after fertilisation, the implanted blastocyst develops three germ layers, the endoderm, the ectoderm and the mesoderm, and the genetic code of the father becomes fully involved in the development of the embryo; later twinning is impossible. Additionally, interspecies hybrids survive only until gastrulation and cannot further develop. However, some human developmental biology literature refers to the *conceptus* and such medical literature refers to the "products of conception" as the post-implantation embryo and its surrounding membranes.[29] The term "conception" is not usually used in scientific literature because of its variable definition and connotation.

Insects[edit]

Red-veined darters (*Sympetrum fonscolombii*) flying "in cop" (male ahead), enabling the male to prevent other males from mating. The eggs are fertilised as they are laid, one at a time.

Insects in different groups, including the Odonata (dragonflies and damselflies) and the Hymenoptera (ants, bees, and wasps) practise delayed fertilisation. Among the Odonata, females may mate with multiple males, and store sperm until the eggs are laid. The male may hover above the female during egg-laying (oviposition) to prevent her from mating with other males and replacing his sperm; in some groups such as the darters, the male continues to grasp the female with his claspers during egg-laying, the pair flying around in tandem.[30] Among social Hymenoptera, honeybee queens mate only on mating flights, in a short period lasting some days; a queen may mate with eight or more drones. She then stores the sperm for the rest of her life, perhaps for five years or more.[31][32]

Fertilisation and genetic recombination[edit]

Meiosis results in a random segregation of the genes that each parent contributes. Each parent organism is usually identical save for a fraction of their genes; each gamete is therefore genetically unique. At fertilisation, parental chromosomes combine. In humans, $(2^{22})^2$ = $17.6\text{x}10^{12}$ chromosomally different zygotes are possible for the non-sex chromosomes, even assuming no chromosomal crossover. If crossover occurs once, then on average $(4^{22})^2$ = $309\text{x}10^{24}$ genetically different zygotes are possible for every couple, not considering that crossover events can take place at most points along each chromosome. The X and Y chromosomes undergo no crossover events[*citation needed*] and are therefore excluded from the calculation. The mitochondrial DNA is only inherited from the maternal parent.

Parthenogenesis[edit]

Organisms that normally reproduce sexually can also reproduce via parthenogenesis, wherein an unfertilised female gamete produces viable offspring. These offspring may be clones of the mother, or in some cases genetically differ from her but inherit only part of her DNA. Parthenogenesis occurs in many plants and animals and may be induced in others through a chemical or electrical stimulus to the egg cell. In 2004, Japanese researchers led by Tomohiro Kono succeeded after 457 attempts to merge the ova of two mice by blocking certain proteins that would normally prevent the possibility; the resulting embryo normally developed into a mouse.[36]

Allogamy and autogamy[edit]

Allogamy, which is also known as cross-fertilisation, refers to the fertilisation of an egg cell from one individual with the male gamete of another.

Autogamy which is also known as self-fertilisation, occurs in such hermaphroditic organisms as plants and flatworms; therein**, two gametes from one individual fuse.**

Other variants of bisexual reproduction[edit]

Some relatively unusual forms of reproduction are:[37][38]

Gynogenesis: A sperm stimulates the egg to develop without fertilisation or syngamy. The sperm may enter the egg.

Hybridogenesis: One genome is eliminated to produce haploid eggs.

Canina meiosis: (sometimes called "permanent odd polyploidy") one genome is transmitted in the Mendelian fashion, others are transmitted clonally.

Benefits of cross-fertilisation[edit]

The major benefit of cross-fertilisation is generally thought to be the avoidance of inbreeding depression. Charles Darwin, in his 1876 book *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom* (pages 466-467) summed up his findings in the following way.[39]

“It has been shown in the present volume that the offspring from the union of two distinct individuals, especially if their progenitors have been subjected to very different conditions, have an immense advantage in height, weight, constitutional vigour and fertility over the self-fertilised offspring from one of the same parents. And this fact is amply sufficient to account for the development of the sexual elements, that is, for the genesis of the two sexes.”

In addition, it is thought by some,[40] that a long-term advantage of out-crossing in nature is increased genetic variability that promotes adaptation or avoidance of extinction (see Genetic variability).

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