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Cell biology and functional dynamics of the mammalian sperm surface

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ABSTRACT

Theriogenology has now a 40-year rich history on covering sperm biological aspects with a special emphasis on farm and husbandry animals. The major and most influential of these contributions will be placed into an evolutionary perspective of ongoing and intriguing progresses made in this field. Although many molecular details have been published, it is more the aim of this contribution to provide a guide through the main established aspects and concepts of sperm surface biology and refer only to major molecular players and mechanisms involved in sperm physiology. Those interested in more molecular details and in-depth knowledge can easily access the most relevant literature which is included here for reference purposes. With this approach, a logical and easy to follow buildup can be made of the general picture of sperm surface dynamics and of the ergonomics of sperm physiology and their function in mammalian fertilization. Understanding the ins and outs of sperm surface biology and the dynamics thereof, might challenge future researchers to design novel generation of better sperm-handling procedures. This could be beneficial for assisted reproductive technology and animal breeding industries.

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1. Introduction

The sperm cell is capable of fertilizing the oocyte and by doing so can form an omnipotent stem cell, the zygote. In the zygote, the paternal and maternal haploid genomes are unified into a unique diploid genome, which will ultimately form a new individual organism. In mammals, fertilization takes place deep in the female genital tract (in the oviduct, at the ampulla [1]) and this process has been optimized for each species in a very sophisticated way during evolution. Consequently, each species has its own fully adapted internal fertilization with remarkable divergences with regard to the following: proteins on the sperm surface involved in fertilization, sperm shapes to allow species-adapted sperm migration and penetration of the extracellular vestments protecting the oocyte,

seminal plasma compositions (and even variations in glands that produce accessory fluids), and a high degree of interspecies variations in number of sperm cells produced per ejaculate and its total volume. Interspecies variations on testis and epididymis size and properties are known, sometimes with seasonal varying size and sperm production that can be photoperiod-dependent [2,3]. Also, in the female tract, variations and morphological specifications are well described although in general, similar mechanisms aid inseminated sperm cells toward the ovulated cumulus–oocyte complex [4]. Moreover, the side where sperm cells are deposited during ejaculation varies to a large extent between mammalian species [5–7]. Beyond this, female animals can be monoestrous (e.g., most primates, bovine) or polyestrous (e.g., porcine, most rodents).

Despite this high degree of speciation in internal fertilization between different mammals, a number of processes are shared in all mammals, albeit that temporal and spatial organization may differ to a large extent for

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different species [8]. The common mechanisms in fertilization operative in all mammals when the sperm cells become ejaculated and deposited somewhere in the female tract are as follows: (1) sperm cells need to become activated and this occurs predominantly in the oviduct (sperm capacitation) [9]; (2) this results in a hyperactivated motility pattern because of changes in metabolism and intracellular signaling cascades [10]; and (3) capacitation also results in the readiness of sperm cells to bind to the extracellular vestments of the oocyte (the cumulus layer and the zona pellucida) and to eventually fertilize the oocyte (see Fig. 1; Refs. [11–16]).

In this review, the sperm cell, as the entity to transform the oocyte after fertilization into an omnipotent zygote, is placed into the spotlight. To enable this very specific task and to ensure the best phenotypic offspring, a number of adaptations have occurred in which the terminally differentiated sperm cell differs from its meiotic and mitotic germ precursor cells in the testis. Understanding these highly ergonomic adaptations of the mature sperm cell will ease us to further study the physiology of the process of fertilization—the only task sperm cells are predetermined to accomplish. Moreover, this overview might help researchers to understand, on one hand, that due to the specific features of sperm, certain molecular biological approaches are very difficult to apply on sperm cells to unravel their physiological roles due to the lack of transcriptional and translational machinery and the lack of a

number of cell organelles [17]. However, on the other hand, the effect of sperm handling can easily be monitored with respect to quite a number of functional readouts such as detection of hyper-activated motility, imaging sperm surface alterations, measuring zonabinding, monitoring the acrosome reaction, and assessing the fertilization rates which can serve as bioassays to study the importance of certain proteins [18].

2. Sperm cell formation in the testis

As mentioned in section 1, the sperm cell is a highly specialized cell and a number of its characteristic features become apparent when, after the second meiotic division of spermatocytes, the formed spermatids are elongated and become sperm-shaped. During the so-called cap phase, the acrosome is formed which—in the mature sperm cell—overlies the apical part of the elongated nucleus, and contains a matrix of enzymes required to enable the sperm cells to reach the oocyte's surface through cumulus layers and the zona pellucida [11,18]. A characteristic condensation of chromatin takes place during the elongation period of spermatids [19]. The DNA condensing histones are removed and replaced by protamines, resulting in a super-condensed DNA. During this phase also, the formation of the tail and its flagellum takes place with the concentration of approximately 100 mitochondria at the midpiece (where they are spirally wrapped around the central flagellum) that will be responsible for the aerobic functioning of the sperm cell [20]. More distal on the sperm tail, the principal piece contains no mitochondria but a specific set of dense cytoskeletal adaptations around the central flagellum to ensure forward movement properties [21,22]. The most distal end piece contains essentially the central flagellum surrounded by the plasma membrane. Just before the sperm cell is liberated from the luminal surface of its guiding Sertoli cell, it has shed off a number of organelles and cellular processes.

Most of the cytosol and redundant organelles such as Golgi complexes, endoplasmic reticulum, lysosomes, peroxisomes, and ribosomes are removed, because they are not acquired for maintenance of the sperm cell and/or for the fertilization of the oocyte [23]. Thus the sperm cell is not able to *de novo* produce proteins. Moreover, due to the absence of membrane vesicle transport (with the exception of the very specific acrosome reaction which will be dealt with in section 5.), no recycling of sperm surface proteins is allowed in the mature sperm cell. As a result, the sperm surface is very inert from a molecular biological point of view. Despite this fact, the sperm surface is very interesting from a cell biological point of view, as despite the molecular biological silencing of the sperm cell at spermiation, it already has a polarized organization of intracellular organelles. The overlying plasma membrane probably has differential interactions with these underlying structures and, as a result, has an appearance of membrane subdomains that can easily be distinguished even in testicular sperm cells [18]. The sperm cell is prone to a very complex and lengthy voyage through the male and female genital tract [24]. During this voyage, the sperm surface is extensively processed by

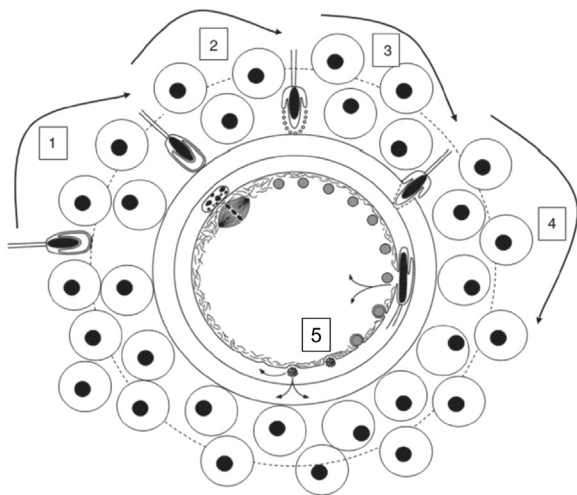


Fig. 1. Fertilization of the mammalian oocyte. The capacitated sperm cell (1) binds either at the level of the cumulus layer or at the zona pellucida (2) this results in the initiation of the acrosome reaction [11]. (3) Both the exposure of the acrosomal content, which is capable to lyse extracellular matrices of the cumulus and/or the zona pellucida, and the hyper-activated motility (necessary for drilling the sperm cell through these extracellular matrices) are required for allowing a few sperm cells to reach the perivitelline space [11]. (4) Normally one sperm cell is the first to adhere to the oocyte's surface and to fuse with that and thus fertilize the oocyte [12]. (5) The now fertilized oocyte immediately acts to prevent another sperm cell to fuse and thus prevents polyspermic fertilization. To this end the fertilized oocyte over the entire surface allows a cortical reaction in which the cargo of the cortical granules (secretory granules just underlying the oolemma) are secreted and alter the properties of the zona pellucida and the oolemma [13,14]. The fertilizing sperm cell brings the signal for oocyte activation and thus also causes polyspermy blockage [15,16].

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