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Current knowledge on boar sperm metabolism: Comparison with other mammalian species

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ABSTRACT

A practical consequence of the specific pig reproductive cycle is that the main functional features that distinguish boar spermatozoa cannot be extrapolated to other species. This prevents an overall picture that explains mammalian sperm function from being assumed. Furthermore, the extraordinary complexity of the molecular mechanisms implied in the control and modulation of mature boar sperm functions makes it impossible to provide a complete description of these mechanisms in the limited space of this chapter. Taking this into account, this chapter centers on the description of three highly important specific aspects of boar sperm function. The first aspect is the mechanisms by which boar sperm cells uptake extracellular energy sources. The second aspect is the necessity of mammalian sperm to use other hexoses than glucose as feasible energy sources. The third aspect would be an analysis of the roles that mitochondria could play in the regulation of the overall boar sperm function. As a whole, this revision intends to be an overall picture of regulatory mechanisms involved in the maintenance of proper energy levels of boar sperm and their relationship with the control of the overall boar sperm function.

1. Overview of mammalian sperm energy metabolism

Mammalian spermatozoa are very specialized cells, which show unique features not only when compared with other cells but also when compared among species. Differences among species are obvious from practically all of the aspects that we used to compare them. Thus, aspects like sperm head morphology or specific motion parameters are very different among species [1,2]. The main reason for these differences lies in the existence of specific, much-differentiated, reproductive evolutionary strategies among species. These strategies imply that questions such as the lifetime of spermatozoa inside the female genital tract can vary enormously, from a few hours (i.e., bovine) to several months (i.e., pteropodidae; see [3]). Other important points that modulate mammalian sperm function would be those related to the existence of male competition, the time lapse of the estrous period, and even the volume of the ejaculate [4–6]. In this manner, each mammalian sperm cell must be adapted in all of its aspects, from morphology to molecular mechanisms of function control, depending on the strict reproductive requirements of each species.

Focusing on pig reproduction, boar sperm is designed to reach optimal fecundation rates in a system that comprises a 2- to 4-day-long estrus period, a multiple fecundation process, an ovulation facilitated by the contact of ejaculate with the sow genital tract and a very large ejaculate volume. These facts imply that the optimal boar sperm must accomplish several requisites that allow it to be fully functional. Among these requisites, two are relevant for the

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purpose of this review. The first of them is the modulation of a specific motility pattern from ejaculation to oviduct colonization. The second of these requisites is the regulation of the sperm energy metabolism to obtain the maximal efficiency to sustain a relatively long life span period, which would coincide with the estrous time lapse.

The mean boar sperm motility of freshly obtained samples is appreciably slower than that determined in other mammalian species such as horses, dogs, bulls, or mice (See [7–11] as examples.) One of the most plausible explanations, if not the most for this phenomenon, would be based on the exact semen deposition place. Thus, boar sperm is deposited much closer to the oviduct than is of other mammals such as dogs or horses. This avoids boar sperm having the necessity to move quickly through areas of the female genital tract that are very harmful for them, such as the anterior area of the vagina and cervix. In this respect, we must remember that the semen deposition area of many species is precisely the aforementioned ones, which present a very strong immune response against spermatozoa. Furthermore, the great volume of boar ejaculate, combined with the contraction movements of the sow uterus during estrus, lessens boar sperm activity to reach the appropriate uterine grooves that will channel sperm transit to the oviduct (See [12] as a review.) However, the fact that boar sperm presents lower levels of motility than, for example, dog sperm, will imply that the energy management that ultimately causes this specific type of movement has to be different from that of other species. But, what are the main differences among energy management in species? If we compare two species such as boars and dogs, which present very separate characteristics in aspects such as motility and life span in the female genital tract, we can try to clarify these differences.

Energy management of mammalian sperm is based on the control of two main aspects. The first aspect is the obtainment of energy from external sources. The second aspect is the yielding of energy from intracellular stores. On the one hand, the main energy-producing mechanisms from external sources that mammalian sperm present are based on the processing of monosaccharides through the glycolytic pathway and the subsequent metabolization of sugar-derived metabolites through mitochondrial oxidative phosphorylation. On the other hand, the main energy-producing pathway of internal stores will be the degradation of glycogen deposits to glucose that will be further processed to glycolysis and, eventually, subsequent mitochondrial oxidative phosphorylation. There are, of course, other energy sources available for sperm. Thus, extracellular metabolites such as lactate, pyruvate, citrate, glycerol, and even triglycerides have been reported as external energy sources for sperm from species such as boars [13–15]. However, without dismissing the importance of these metabolites as important energy sources, the lack of further knowledge regarding the use of these nonsugar metabolites restrains a more in-depth discussion about them.

2. How does mammalian sperm enter extracellular hexoses in their cellular energy production system?

Regarding the glycolysis pathway, the regulation of this very important metabolic pathway is complex. In this way, variations in the intracellular levels of a wide variety of intracellular factors such as ADP, ATP, AMP, pH, or intracellular oxygen pressure are potent regulators of the glycolytic flux rhythm (See [16] as a review.) The majority of these factors act through modifications of the enzymatic activity of several key points in the pathway. In this manner, there are several key modulating points inside the glycolytic enzymatic cascade that should be considered to understand the regulation mechanisms involving this pathway. Among these regulatory points, perhaps the most important are those linked to the control of the uptake and subsequent phosphorylation of monosaccharides together with those controlling the way by which the final product of the glycolytic flux, pyruvate, will be subsequently processed [16].

Cell monosaccharides uptake is controlled by two separate families of specific hexose transporters, the GLUT family and the SGLT family [17,18]. Although proteins of the SGLT family have been reported to be present in mammalian sperm [19], at this moment, there is a general consensus in considering that GLUT proteins are the most important hexose uptake mechanism of mammalian sperm [20].

The GLUT family proteins are hexose transporters that are universally present in all cellular types [17,18]. They passively transport hexoses and, with minor affinity, other substrates such as vitamins and amino sugars [17,18]. Because they are passive transporters, no energy consumption is required for the correct functioning of these proteins, which work based on a gradient system [17,18]. At this moment, there are a minimal of 14 separate described GLUT proteins, which are numbered from 1 to 14. These proteins differentiate themselves by subtle structural changes that, in turn, lead to great differences in the affinity for separate sugars and tissue specificity [17,18]. Regarding mammalian spermatozoa, the GLUTs that have been detected until now comprise GLUT-1, GLUT-2, GLUT-3, GLUT-5, GLUT-8, and GLUT-9, whereas the presence of the insulin-dependent GLUT-4 seems doubtful [20]. An intriguing question regarding GLUTs is why a cell, such as the mature mammalian spermatozoon, requires the presence of at least six separate GLUT hexose transporters to uptake a very common external energy sources such as monosaccharides. This question is even more difficult to explain if we consider that these GLUTs have separate affinities for each monosaccharide. This is a question that, in fact, is linked to another very intriguing characteristic involving sperm function, namely, the use of monosaccharides, other than glucose, as energy sources by mammalian sperm. Thus, although glucose is present in the seminal plasma of practically all of the studied species so far [16], many species present other monosaccharides as a common substance. Thus, fructose is present in many species [21], although this sugar is not the most abundant sugar in species such as boar or bull [22]. Even more strange, substances such as sorbitol are present in the seminal plasma of species such as horse [23]. Arriving at this point, we must remember that sugars such as fructose or sorbitol are very rarely found in animal tissues. In this way, the presence of monosaccharides such as fructose and sorbitol in an animal tissue such as seminal plasma can