



Review

Cross-talk between free and bound spermatozoa to modulate initial sperm:egg ratios at the site of fertilization in the mammalian oviduct

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ABSTRACT

This essay proposes that highly localized communication between free and bound spermatozoa in the caudal portion of the oviduct acts to regulate the numbers detaching from the epithelium and progressing to the site of fertilization close to the time of ovulation. Low initial sperm:egg ratios are essential for monospermic fertilization. Liberation of surface macromolecules and metabolic prompting from activated spermatozoa, together with altered patterns of sperm movement and dynamic differences in intracellular Ca^{2+} ion status between neighboring sperm cells, would influence the progressive release of spermatozoa from the reservoir in the oviduct isthmus. Different intensities of preovulatory epithelial binding, reflecting a range of states in the sperm surface membranes and associated proteins, would provide a further explanation for a chronologically staggered periovulatory detachment of spermatozoa. Intimate sperm–sperm interactions within the confines of the oviduct isthmus offer a sensitive means of fine-tuning the vanguard of competent male gametes reaching the isthmo-ampullary junction.

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1. Introduction

In recent years, competition between spermatozoa in the female genital tract before fertilization has emerged as a prominent theme within the discipline of reproductive biology [1–7]. One inference has been that those spermatozoa directly involved in the events of fertilization are in some manner ‘superior’. In eutherian mammals, such putative superiority has generally been attributed to motility characteristics, primarily to the speed of swimming within the female tract [8–11]: the first spermatozoon to reach an egg’s investments is presumed to be the fertilizing spermatozoon. However, if there is indeed some form of

selection of a vanguard of superior spermatozoa, what does this mean genetically? Does the genome of a ‘superior’ fertilizing spermatozoon lead to the generation of a better quality zygote and thereby to a more viable embryo? Although the response to this question remains unknown, the incidence of prenatal mortality in spontaneously breeding mammals is some 30% to 40% [12–16], placing the notion of embryo viability in a realistic perspective.

An understanding of sperm competition that focuses on swimming speeds may overlook considerable subtlety in the nature of sperm interactions before and close to the onset of fertilization. In the respective fields of sperm competition and sperm selection within the female tract of mammals, new insights might be gained by considering the possibility of communication between individual sperm cells *en route* to the site of fertilization. This essay has such an objective and examines the following: (1) where and when sperm–sperm interactions might be found, (2) the

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potential nature of sperm–sperm interactions, and (3) why they could be beneficial.

Sperm cross-talk, as proposed in this article, would not include instances of sperm cooperation [17,18]. In the sense previously used, such cooperation acts to facilitate sperm progression in the lower genital tract, especially in the uterus, rather than acting quantitatively within the oviduct isthmus to regulate sperm release.

2. Where might sperm–sperm interactions occur?

In species in which ejaculation is into the vagina, such as rabbits, ruminants, and primates, nonrandom sperm contacts may have occurred during entry into the cervix and passage through the mucus-lined cervical canal. However, the initial focus of this essay will be on the uterus wherein gradients in the density of suspended spermatozoa are established toward the region of the utero-tubal junction [19]. After the much accentuated myometrial contractions induced at coitus have subsided and as subpopulations escape from immersion in seminal plasma in the anterior vagina and distal portion of the cervix, scope arises for specific sperm–sperm interactions. These may be initiated while in suspension in the lumen of the uterus or close to the endometrial surface and could occur during passage between and across the folds of the utero-tubal junction. Indeed, this specialized junctional region may itself impose a form of selection on those sperm entering the oviducts [19–21].

In species in which the ejaculate is introduced into the uterus at mating (e.g., dog, horse, pig, many rodents), the utero-tubal junction forms distended papilla-like processes that protrude into the uterus during estrus (see Fig. 1 in Ref. [22] and Figs 1 and 2 in Refs [23] and [24]). These processes act primarily as a valve to prevent bulk entry of seminal fluids into the lumen of the oviduct. In such species, vigorous sperm motility is essential for traversing this formidable barrier in the hours before ovulation. During passage across and through the utero-tubal junction, the concentration of suspended spermatozoa is reduced by $X10^2 - X10^3$ (100-fold to 1000-fold) compared with that in the uterine lumen (see Figs in [25,26]). Transient interactions between motile spermatozoa could commence in this region of the tract, as cells proceed intimately across the epithelial surfaces. The nature of such putative cross-talk remains unknown. It might include physical cues concerned with movements of the sperm head and flagellum or molecular interactions concerned with the sperm surface or a combination of both. Each could be mediated by contact with specialized epithelial cells. Sperm-specific proteins may assist passage through the utero-tubal junction [27].

Interactions of an immunological nature are beyond the scope of this essay (see [19,28,29]), but the vast population of polymorphonuclear leukocytes that infiltrates the uterus in response to seminal products needs consideration. Sperm interactions with polymorphonuclear leukocytes take many forms and, as originally proposed Soupart [30], could contribute to modification of the sperm surface and the process of capacitation. Viable spermatozoa are resuspended in female genital fluids during ad-ovarian progression, so the potential for specific sperm–cell interactions should

increase, becoming most effective within the confines of the oviduct isthmus. The potential nature and significance of sperm–sperm interactions in this portion of the tract are considered in subsequent sections.

3. When might sperm–sperm interactions occur?

At this point of the essay, it is appropriate to recall extensive observations on sperm distribution and motility in the oviduct in the hours before and soon after ovulation. Following mating early in estrus and until close to the time of ovulation, highly motile spermatozoa entering the oviducts in laboratory rodents and domestic farm animals are arrested and bind to the epithelium of the caudal isthmus (reviews: [11,19,27,31–36]). Having gained this region of constriction just beyond the utero-tubal junction, spermatozoa undergo suppression of motility in a viscous glycoprotein milieu and make specific adhesion contacts between the sperm head and endosalpingeal cilia or microvilli or both [22,23,37]. A functional sperm reservoir is thereby established. When ovulation is imminent, and with the prospect of one or more oocytes being shed into the oviduct, discrete numbers of competent spermatozoa are activated and released from epithelial binding [27,32,38–40]. This controlled release of subpopulations generates initial sperm:egg ratios at the isthmo-ampullary junction—the site of fertilization—close to unity, reducing the risk of multiple sperm penetration of individual eggs [32,38,40]. Such tight regulation around the time of ovulation should be contrasted with postovulatory release of progressively increasing numbers of motile spermatozoa, although this occurs too late to influence the normality of fertilization: a stable block to polyspermy would have already been established in activated eggs [33,40,42–44].

Overall control of these pre- and periovulatory events within the genital tract resides in endocrine activity of the ipsilateral gonad [32,33,41,45]. Such an influence is mediated through the systemic circulation and, 10 to 20 times more powerfully, *via* a local countercurrent transfer of hormones, notably of progesterone, between the ovarian vein and oviduct branch of the ovarian artery [32,33,40,45]. Periovulatory Graafian follicles close to shedding a female gamete thereby communicate with the region of the oviduct containing a reservoir of male gametes and signal the imminence of ovulation. Binding of spermatozoa to the endosalpinx facilitates transfer of informational cues from the gonad-programmed mucosa *via* intercellular bridges. This ipsilateral endocrine regulation is proposed to act in concert with highly localized sperm interactions as a means of fine-tuning the number of spermatozoa activated and released from binding shortly before and soon after ovulation. Remodeling of the sperm surface, shedding of sperm proteins, and the onset of hyperactive motility may all be critical at this stage [27].

4. Why cross-talk could be beneficial

In this system for the generation of low *initial* sperm:egg ratios at the site of fertilization, a negative feedback influence of detaching and detached hyperactive spermatozoa would act to regulate the reserves of spermatozoa still

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