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INTRODUCTION

The beginning of life is strictly dependent on morphological and biochemical changes that occur in the sperm and the egg as the result of their activation. Fertilization is a popular research topic: studies on a variety of animals and plants have addressed it with a number of experimental approaches, yet, the molecular mechanisms by which the sperm activates the egg are still poorly known. Hopefully, this thematic issue will stimulate new ways to look at the process, and indicate research perspectives that will advance our understanding of the field. It will update information on what is presently known on the fine aspects of the sperm–egg interaction process, and on the molecular mechanisms of egg activation under natural conditions, and will summarize the activation events which are described as polyspermy preventing mechanisms. The comparison of the morphological and biochemical changes that define the signal transduction pathways occurring at the fertilization of different species will highlight the pioneering concept of Ernest Everett Just (1939) according to whom "*there is one feature common to all fertilization-processes we shall see after we have evaluated the differences in the structure of the gametes as well as those in the time and the mode of their union*" [1]. The recent finding of a molecular mechanism for the self-incompatibility system that avoids inbreeding shared by living organisms regardless of their taxonomic position (e.g., flowering plants and ascidians) is particularly relevant to it.

Many of the findings on the fertilization process over the last 150 years have come from marine organisms (mostly echinoderms and tunicates) which synchronously release their gametes in the sea. These eggs have been an exceptional model system to study the molecular mechanism that determines cytoplasmic maturity (oocyte maturation process), the species-specific adhesion of sperm to the egg envelope during fertilization, egg activation as well as the development of the embryo under conditions which reproduce those occurring in nature [2]. A large body of evidence indicates the importance of Ca^{2+} for the activation of the sperm prior to its interaction with the egg. When starfish or sea urchin sperms are added to eggs they undergo the acrosomal reaction upon their interaction with the layers surrounding the eggs. Other dramatic morphological changes in these species include the extension of the filamentous acrosomal process when the sperm encounters the jelly coat, whereas in mammals the prevailing view that the acrosome-intact sperm binds to the zona pellucida of oocytes denuded of their cumulus oophorus cells and then undergoes acrosomal exocytosis has been challenged by work with advanced imaging technology on intact oocytes [3]. At fertilization of sea urchin eggs Ernest Everett Just first described that "*before the actual elevation of the membrane, some cortical changes beginning at the point of sperm entry sweep over the egg, immunizing it to other sperms*" [1]. Electrophysiological and Ca^{2+} imaging studies have later shown that the attachment of the sperm induces a transient Ca^{2+} rise in the egg cortex which is the result of Ca^{2+} entry through voltage-gated channels following membrane depolarization. After the first sperm is bound, the membrane potential shifts to a positive level and some authors have suggested this prevents the fusion of supernumerary sperm [4]. Recent results on starfish eggs are of particularly interest, since the long acrosomal filament emerging from the tip of the successful spermatozoon upon contact with the jelly layer only induces the cortical Ca^{2+} release if the structural organization of the actin cytoskeleton is not injured: rapid changes in the structure of the cortical actin cytoskeleton induced by the first sperm would prevent the attachment of supernumerary spermatozoa and not membrane potential [5]. The findings presented in this issue indeed indicate that the dynamic changes of the actin cytoskeleton in the ectoplasm (outer region of the egg) are likely to regulate the Ca^{2+} changes, the cortical granules exocytosis and sperm incorporation in sea urchin eggs as well. Contributions in this Thematic Issue thus critically re-evaluate the hypothesis of a fast electrical block to polyspermy, and suggest that monospermic fertilization is independent of the egg voltage, but is acquired during oocyte maturation through a cortical organization of actin filaments.

Depending on the species, the intracellular Ca^{2+} increase following egg activation may occur as a single transient or as repetitive Ca^{2+} transients. Following the first visualization of the sperm-induced Ca^{2+} wave, beginning at the site of sperm egg interaction and propagating to the opposite pole in medaka eggs several decades ago, a number of mechanisms have been inconclusively suggested to be responsible for the generation of the Ca^{2+} signals. All known Ca^{2+} mobilizing messengers – $InsP_3$, cADPR, NAADP – have been shown to mobilize Ca^{2+} in echinoderm eggs, albeit with subtile differences. In sea urchins' NAADP has been suggested to trigger Ca^{2+} release from acidic vesicles different from the ER, whereas in starfish the uncaging of injected NAADP triggers a plasma membrane depolarization similar to that induced by the sperm, inducing Ca^{2+} influx through a Ca^{2+} channel. The $InsP_3$ receptors instead appear to be involved in the global mobilization of Ca^{2+}. The Ca^{2+}-dependent elevation of the fertilization envelope (the evolution of which is discussed in the Issue) is the result of cortical granules exocytosis and represents an important aspect of the mechanical barrier to polyspermy. In mammalian fertilization, oocyte activation is linked to the $InsP_3$-mediated periodical Ca^{2+} rises induced by a PLC isoform upon sperm egg fusion. The localization of PLCζ within the egg and the sperm before the initiation of fertilization will be discussed in the Issue. The activation of a Ca^{2+}-calmodulin dependent tyrosine kinase pathway by mouse sperm,

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which is essential for their incorporation and which is downstream of the fertilization-induced Ca^{2+} transients will also be discussed. Eggs and oocytes of various species are arrested at different stages of the meiotic cycle, waiting for the sperm triggered Ca^{2+} signals to release it from arrest: findings related to cell cycle arrest and egg activation in echinoderms and tunicates are also discussed, as are a number of aspects of endoplasmic reticulum dynamics during oocyte maturation and of the calcium signalling at the fertilization of nemertinean and annelidan marine worms.

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