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Review

Calcium and actin in the saga of awakening oocytes

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This review is dedicated to Professor Ernesto Carafoli.

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ABSTRACT

The interaction of the spermatozoon with the egg at fertilization remains one of the most fascinating mysteries of life. Much of our scientific knowledge on fertilization comes from studies on sea urchin and starfish, which provide plenty of gametes. Large and transparent, these eggs have served as excellent model systems for studying egg activation and embryo development in seawater, a plain natural medium. Starfish oocytes allow the study of the cortical, cytoplasmic and nuclear changes during the meiotic maturation process, which can also be triggered *in vitro* by hormonal stimulation. These morphological and biochemical changes ensure successful fertilization of the eggs at the first metaphase. On the other hand, sea urchin eggs are fertilized after the completion of meiosis, and are particularly suitable for the study of sperm–egg interaction, early events of egg activation, and embryonic development, as a large number of mature eggs can be fertilized synchronously. Starfish and sea urchin eggs undergo abrupt changes in the cytoskeleton and ion fluxes in response to the fertilizing spermatozoon. The plasma membrane and cortex of an egg thus represent "excitable media" that quickly respond to the stimulus with the Ca^{2+} swings and structural changes. In this article, we review some of the key findings on the rapid dynamic rearrangements of the actin cytoskeleton in the oocyte/egg cortex upon hormonal or sperm stimulation and their roles in the modulation of the Ca^{2+} signals and in the control of monospermic fertilization.

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1. Starfish and sea urchin eggs as suitable model systems for studying maturation and fertilization

For more than one hundred years, eggs of marine animals have provided favored materials with which to explore the mechanisms of egg activation and embryonic development. When extracted from the gonad during the breeding season, nearly all immature oocytes contain the characteristic large nucleus (termed germinal vesicle, GV) (Fig. 1). Upon interaction with the sperm, these oocytes increase their intracellular Ca^{2+}, but are penetrated by numerous spermatozoa. It was thought that the polyspermic fertilization of immature oocytes was because of their incapability of cortical granules exocytosis and the consequent lack of the elevation of the fertilization envelope, which would mechanically block the entry of supernumerary spermatozoa [1–3]. Successful monospermic fertilizability develops in the maturation process, during which the morphological changes in the surface of the eggs coincide with the breakdown of the germinal vesicle (GVBD) (Fig. 1B). After the first descriptions of oocyte maturation [4,5], the control of starfish maturation has been extensively studied thanks to the identification of the maturing hormone 1-methyladenine (1-MA), which can be easily added to the seawater in which the immature oocytes are suspended [6,7].

A few minutes after hormonal stimulation, a rapid reorganization of the actin cytoskeleton occurs at the oocyte surface, which is accompanied by a Ca^{2+} increase in the cortex and in the GV [8–12]. Later events in the maturation process include the GVBD and the intermixing of the nucleoplasm with cytoplasm, which is essential to trigger the events of cortical maturation that are critically conducive to the successful egg activation by the sperm. The optimal period for fertilizing starfish eggs is between the GVBD and the extrusion of the first polar body. At variance with other egg types, which have a very limited time window during which fertilization is possible, starfish eggs can still be fertilized several hours after the addition of 1-MA. This allows them to be used for studying the cytoplasmic changes that misguide the aging eggs during the fertilization process [13–15].

Unlike starfish that are fertilized as primary oocytes, sea urchin eggs are shed into the seawater after the completion of meiosis i.e., they are fully matured and thus more stable. Much of the knowledge

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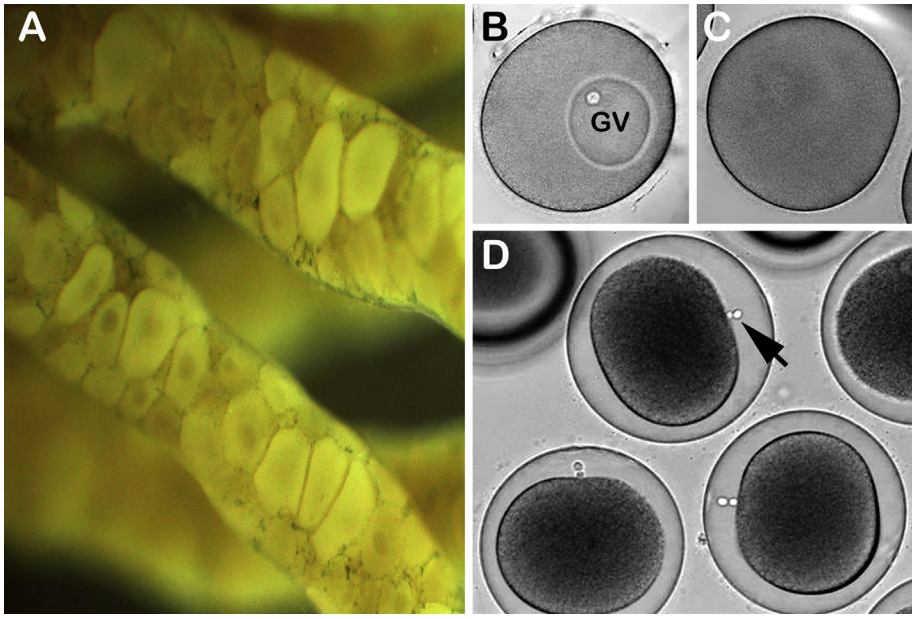

Fig. 1. Starfish oocytes as an experimental model system for studying meiotic maturation and fertilization. (**A**) Dissected female gonads of the Mediterranean starfish *Astropecten aranciacus* in seawater. During the breeding season (February–May), the female gonad provides fully grown immature oocytes that are arrested in prophase I of meiosis. (**B-D**) Meiotic maturation and fertilization of the eggs from *Asterina pectinifera*. (**B**) A transmitted light image of immature oocytes. Note the large nucleus (germinal vesicle, GV) and the small nucleolus inside it. (**C**) Immature oocytes become mature eggs after the treatment with 1-MA: at this stage of maturation, GV breakdown has taken place, and the nucleoplasm is intermixed with the cytoplasm. (**D**) A transmitted light image of the fertilized eggs. Note the elevation of the fertilization envelope. Regardless of fertilization, the first and second polar bodies are extruded from the animal pole respectively 70 and 90 min after the stimulation with 1-MA (arrow).

on the fast events of sperm–egg interaction originated from the studies of sea urchin eggs. Within seconds after the addition of active spermatozoa, rapid structural changes take place in the egg following the liberation of Ca^{2+} and the elevation of the fertilization envelope, the latter of which is the consequence of cortical granules exocytosis. The importance of Ca^{2+} during the process of oocyte maturation and fertilization has been confirmed in numerous animal species, and the detailed signal transduction pathways that lead to the intracellular Ca^{2+} liberation during hormonal and sperm stimulation have been most extensively studied with starfish and sea urchin. This review article will focus on these two marine animals to describe the roles of the cortical actin cytoskeleton in modulating sperm–egg interaction and Ca^{2+} signals [16–18].

2. Changes of the actin cytoskeleton during the maturation of starfish oocytes

In the starfish ovary, immature oocytes are ensheathed with the vitelline and jelly coats over the plasma membrane, and are associated with a thin layer of follicle cells. The application of 1-MA induces detachment of the follicle cells from the oocytes surface and their migration and concentration in one side of the mature egg. The starfish ovary undergoes a marked contraction at spawning due to the operation of the smooth muscles present in the ovarian wall. As expected of a muscle contraction process, this contraction does not occur in the absence of Ca^{2+} in seawater [7]. The average diameter of fully grown oocytes is about 250 μm for the Mediterranean species *Astropecten aranciacus*, and 180 um for the Japanese species *Asterina pectinifera*. As aforementioned, these oocytes contain a large GV (80–100 μm in diameter) with a nucleolus (Fig. 1C). The position of the GV defines the animal pole of the oocyte where polar bodies are extruded during meiosis (Fig. 1D, arrow). Immunofluorescence using anti-α-tubulin antibody has shown that the anchorage of the GV to the animal cortex is controlled by microtubular structures, which is essential for the normal course of meiotic events [19]. However, in addition to the microtubule-mediated nuclear positioning, we have found that actin filaments are also intimately associated with the surface of the GV, which may play a role in anchoring the GV at the animal pole (Fig. 2B).

1-MA acts on the surface of the oocyte from outside, as it is inactive when injected into the cytoplasm [20]. It is assumed that 1-MA interacts with the cell surface receptor belonging to the G-protein-coupled receptor family [21,22]. This triggers the maturation process through the activation of the Maturation Promoting Factor (MPF) which turned out to be the cyclin B-Cdc2 kinase (Cdk1) complex that serves as the universal activator of the meiotic and mitotic cycles [23,24]. The intracellular mediator of 1-MA stimulation has been identified as the phosphorylated (and activated) protein kinase AKT (protein kinase B, PKB) which in turn phosphorylates and suppresses the inhibitory activity of Myt1. As a member of the Wee1 family of protein kinases, Myt1 upregulates the Ca^{2+}-dependent Cdc25 phosphatase which in turn activates cyclin B-Cdc2 [25,26]. The GVDB of the starfish oocyte requires at least 8 min exposure to 1 μM 1-MA, and its onset varies depending on the species. The length of this so-called 'hormone-dependent period (HDP)' is not dependent on the hormone concentration, but the removal of the hormone during HDP interrupts maturation. Beyond the HDP, however, the maturation process irreversibly proceeds even in the absence of 1-MA [27–30]. Curiously, oocyte maturation in starfish can also be induced by disulfide-reducing agents (e.g. dithiothreitol). They mimicked 1-MA in inducing morphological changes and an increase of the sulfhydryl contents in the proteins of the oocyte cortex [31].

Light and electron microscopic studies have revealed cortical changes as early as 1 or 2 min after 1-MA addition that are linked to the structural reorganization of the actin cytoskeleton: microvilli retraction, alignment of the cortical granules with their longer axis perpendicular to the plasma membrane, and the formation of surface spikes that contain bundles of actin filaments. These structures, which are generated by rapid, reversible polymerization

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