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Ion currents involved in gamete physiology

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ABSTRACT Gametes are electrogenic cells that modify their electrical properties in response to different stimuli. This behavior is due to the occurrence of ion currents flowing through ion channels located on the plasma membranes. The modulation of ion channels has been described during the processes of gamete maturation, activation and fertilization in most of the animal models studied. In particular, predominant ions involved in physiological events in oocyte and sperm have been recognized to be sodium, potassium and calcium. In this review, we give an overview on the occurrence, modulation and function of ion fluxes, from gametogenesis to early fertilization events, from marine animals to human. The implications for a dynamic role of ion currents in gamete physiology and their possible clinical and technological applications are discussed.

KEY WORDS: *gamete, ion channel, ion current, oocyte, spermatozoa*

Introduction

Main steps of the reproductive process are the production of the two gametes (spermatogenesis and oogenesis), their reciprocal activation and the following interaction (e.g. fertilization). Gametogenesis is underlined by meiosis, the unique process of cell division which provides the formation of haploid spermatozoa and oocytes. Gamete maturation is the last phase of gametogenesis and transforms immature cells in gametes competent for fertilization. This is the highly specialized process of cell interaction and signal transduction that generates a new individual of the same species through different events, such as recognition, binding and fusion of the two gametes. These events are also accompanied by a still unclear process that is the reciprocal activation of the gametes. First the spermatozoon is activated by the signals coming from the oocyte extracellular membranes, that induce changes either in the shape and function of the spermatozoon rendering it a motile and fusible cell and attracting it toward the oocyte. At the end of the sperm activation and just after the fusion of the two plasma membranes, the spermatozoon starts to activate the oocyte by inducing calcium (Ca^{2+}) oscillations (Gillot *et al.,* 1990; Swann and Yu 2008) transforming its quiescence into a metabolic activated state up to cell cycle resumption (Dupont *et al.,* 2010) that in turn triggers the program of development (Yanagimachi 1994).

Gametes are excitable cells which, during the processes of maturation and fertilization, undergo transient modifications of the electrical properties due to the activity of ion channels present on their plasma membrane. The modulation of ion channels have been widely demonstrated on the oocytes and spermatozoa of all the animals studied (Darszon *et al.,* 2001; Hagiwara and Jaffe 1979; Tosti and Boni 2004; Tosti *et al.,* 2013). The modifications in the plasma membrane asset have been historically first studied in marine invertebrates and then extended to mammals and human.

In this review, we will describe the presence and activity of currents flowing through the ion channels in the oocyte and spermatozoon and in the early stages which follow their interaction in the most studied animal species from marine invertebrates to human (Figs. 1,2).

Why study the plasma membrane?

The plasma membrane marks the borderline between inner and outer compartments of the cell. On the gamete plasma membrane there are located all the molecules (ligand and receptors) responsible for the events of recognition, binding and fusion. Ion channels are among these molecules and their involvement in the functionality of gametes is a matter of intense study. The plasma membrane is the site of a difference of electrical charge distribution that creates an electrical gradient named voltage. The voltage difference across the plasma membrane creates a store of potential energy that give rise to a trans-membrane potential known as resting potential.

Every excitable cell has a specific resting potential that is normally negative ranging from -10 millivolt (mV) to -100 mV (DeFelice

Abbreviations used in this paper: AQP, aquaporin; AR, acrosome reaction; Ca^{2+}, calcium; Cl^-, chloride; FC, fertilization current; GV, germinal vesicle; GVBD, germinal vesicle breakdown; K^+, potassium; MI, metaphase I; MII, metaphase II; Na^+, sodium.

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