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Sperm-triggered Calcium Oscillations at Fertilization

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Summary. Reinitiation of embryonic development at fertilization is brought about by a sperm-triggered rise in egg cytosolic calcium (Ca^{2+}) levels. Three models of how sperm trigger this Ca^{2+} increase have been proposed: the conduit, contact and content models of fertilization. Overwhelming evidence indicates that the Ca^{2+} -releasing second messenger inositol 1,4,5-trisphosphate (InsP_3) is produced at fertilization. The task ahead will be to determine how egg phospholipase $\text{C}\gamma$ is activated at fertilization to generate InsP_3 . Although sperm trigger the initial Ca^{2+} rise in the egg, maternal factors determine whether the Ca^{2+} rise will be a solitary transient or else a series of oscillations. This is important since a solitary Ca^{2+} spike within physiological limits is not a sufficient stimulus for meiotic exit in ascidians. It is likely that the egg cyclin B-dependent kinase (Cdk1) activity determines whether the egg displays one Ca^{2+} transient or a series of Ca^{2+} oscillations; persistently elevated Cdk1 activity prolongs the duration of sperm-triggered Ca^{2+} oscillations indefinitely. Partly because of this finding, but also since all the sperm-triggered Ca^{2+} oscillations are Ca^{2+} waves that display a predictable temporal pattern and spatial organisation, the ascidian has become an excellent testing ground for the various models of fertilization. Cytosolic extracts prepared from *A. aspersa* sperm injected into homologous eggs mimic fertilization using these three criteria: temporal pattern, spatial organisation, and regulation by egg Cdk1 activity. We therefore suggest that the content (sperm factor) model best explains fertilization in ascidians.

Key words. Fertilization, Ca^{2+} oscillations, Cdk1 activity, Content model

Introduction

Sperm reinitiate embryonic development at the moment of fertilization by triggering an increase in egg cytosolic calcium (Ca^{2+}) levels (Ridgeway et al. 1977; Steinhardt et al. 1977). In many animals these Ca^{2+} increases often take the

form of oscillations (mammal: Cuthbertson et al. 1981; ascidian Speksnijder et al. 1989a; starfish: Stricker 1995; annelid: Eckberg and Miller 1995; mollusc: Deguchi et al. 1996; nemertean: Stricker 1996; reviewed by Sardet et al. 1998 and Stricker 1999). In both mammalian and ascidian eggs it has been demonstrated that Ca^{2+} oscillations are the trigger that reinitiates embryonic development (mammal: Kline and Kline 1992; ascidian: McDougall and Sardet 1995; Arnoult et al. 1996; Yoshida et al. 1998).

This review will address two issues. Firstly, how sperm initiate this Ca^{2+} rise in the egg - what molecules are involved? And secondly, how these Ca^{2+} oscillations are maintained by the egg and finally switched off at the end of meiosis when they are no longer required.

Models of Fertilization

For about a decade there have been three hypotheses of how sperm trigger Ca^{2+}

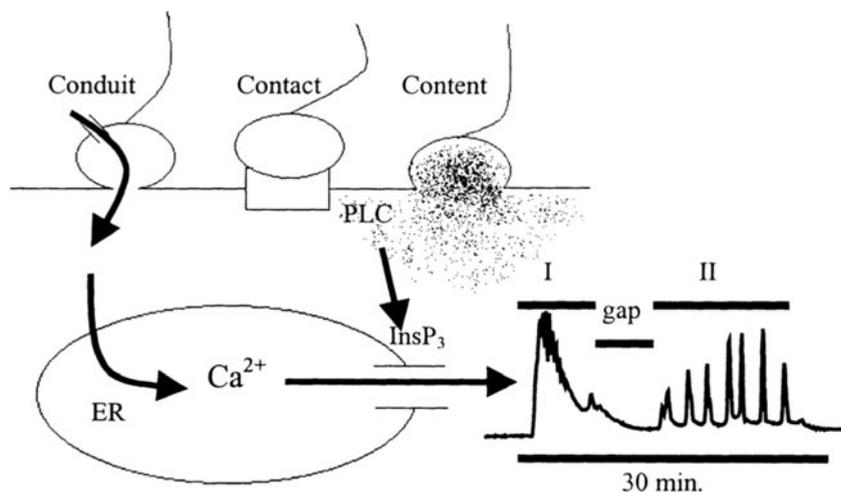


Fig. 1. Models of fertilization and the pattern of calcium oscillations displayed at fertilization in ascidians. Sperm are depicted interacting with the surface of the egg. The conduit model, contact model and content models are displayed. A typical calcium oscillation pattern at fertilization is also displayed (*A. aspersa*). The first and second phases of calcium oscillations (I and II) together with the gap are displayed (calcium oscillations are normally absent or are small during the gap (both phenomena are displayed here)). ER, endoplasmic reticulum, PLC, phospholipase C, InsP_3 , inositol 1,4,5-trisphosphate.