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Ovarian follicle development in vitro and oocyte competence: advances and challenges for farm animals

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ABSTRACT

During the last 2 decades, research on in vitro preantral follicle growth and oocyte maturation has delivered fascinating advances concerning the knowledge of processes regulating follicle growth and the developmental competence of oocytes. These advances include (1) information about the role of several hormones and growth factors on in vitro activation of primordial follicles; (2) increased understanding of the intracellular pathway involved in the initiation of primordial follicle growth; (3) the growth of primary and secondary follicles up to antral stages; and (4) production of embryos from oocytes from in vitro grown preantral follicles. This review article describes these advances, especially in regard farm animals, and discusses the reasons that limit embryo production from oocytes derived from preantral follicles cultured in vitro.

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1. Introduction

In 1996, the birth of 1 live mouse produced through in vitro growth of primordial follicles was the main achievement in mammalian species [1]. Seven years later, this same group reported the birth and survival to adulthood of 59 mice, generated through modification of their original methods [2]. Many researchers have also been committed to develop similar strategies for domestic animals and endangered species, and several reports on the field of in vitro development of preantral follicles, that is, primordial, primary, and secondary follicles, have been published [3–17]. The state-of-the-art of this technique was described in various articles [18–25], but the number of embryos produced from in vitro grown preantral follicles is very low and no gestation was reported. Recently, significant new information has been obtained about gene expression and factors that play crucial roles in in vivo and in vitro oocyte and follicle development in domestic animals, which justifies a new update.

To understand the impact of culturing follicles at early stages of development, it is important to consider that, in most mammalian species, thousands of primordial follicles are present in the ovaries of newborn females and such oocytes could potentially be recovered and cultured in vitro up to maturation. It is known that, by degeneration of the oocyte, many of these relatively quiescent follicles are gradually lost in vivo [26], which dictates the process of reproductive aging [27]. The molecular mechanisms controlling the balance between the survival and loss of primordial follicles have been intensively investigated. In an attempt to understand the mechanisms that control preantral follicle growth, the effects of hormones, local growth factors, and their intracellular signaling pathway have received increasing attention in recent years [28–30]. These studies have contributed for a better understanding of the process involved in folliculogenesis and oocyte maturation.

Oocyte quality and quantity are fundamental for increasing the effectiveness of assisted reproductive techniques, but the oocyte needs to acquire a series of

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competencies during follicular development to make it ready to be fertilized. In the 21st century, several attempts to produce competent oocytes from in vitro grown preantral follicles were described in domestic animals (cow: [31–33]; sheep: [34,35]; goat: [15–17]; buffalo: [24,36]; and pig: [37]). However, in vitro production of fertilizable oocytes and embryos from these livestock animals is still at a low level of efficiency [15,37,38], compared with that from murine species [2]. Part of the problem is due to the complexity of molecular events, in which various hormones and growth factors are involved during the control of oocyte and follicle growth and differentiation at different stages.

The current review updates the knowledge on expression of several growth factors and their receptors in primordial, primary, and secondary follicles and discusses intracellular signaling pathways that control early follicular growth. Furthermore, the effects of various hormones and local factors on preantral follicles, the main advances regarding in vitro maturation of oocytes from early follicles, and the reasons that limit embryo production from in vitro grown oocytes are discussed.

2. Gene expression in preantral follicles from farm animals

The expression of messenger RNA (mRNA) and proteins for receptors of follicle stimulating hormone (FSH), luteinizing hormone (LH), and growth hormone, as well as for several growth factors, like kit ligand (KITLG), epidermal growth factor (EGF), growth differentiation factor 9 (GDF9), bone morphogenetic protein 6 (BMP6), BMP15, platelet derived growth factor, activin A, transforming growth factor β (TGFβ), insulin-like growth factor 1 (IGF1), IGF2, anti-Mullerian hormone (AMH), vasoactive intestinal peptide (VIP), fibroblastic growth factor 2 (FGF2), FGF7, FGF8, FGF10, FGF17 and their receptors in primordial, primary and secondary follicles from farm animals is shown in Table 1 ([11,15,17,39–84]). For small ruminants, an increase in the levels of (*BMP6*) mRNA was reported during the transition from caprine primordial into primary follicles [60]. In addition, during the transition from the primary into the secondary follicle stage in caprine species, an increase in the levels of mRNA for *KITLG* [85], *EGF* [86], *BMP15* [87], *GDF9* [88], and *VIP* [89] has been observed. However, no significant changes in the levels of mRNAs for *IGF1* [90], *FGF2*, [91], and *FSHR* [15] were demonstrated during early follicular growth in goats. In ovine species, Feary et al [62] demonstrated that expression of *GDF9* mRNA in oocytes increases approximately 2-fold during the transition from primordial into primary follicles, whereas the levels of *BMP15* mRNA in oocytes double as follicles progressed from primary to large secondary follicles. These authors also reported that concentrations of *BMPR1B* mRNA in oocytes and granulosa cells reach a peak in primary follicles, with expression being lower in large secondary follicles. The levels of *BMPR2* mRNA in granulosa cells increase slightly between primordial and primary follicles but fell significantly in secondary follicles [62]. In addition, the expression of *TGFβR1* mRNA in granulosa cells doubles between primordial and small secondary follicles [62]. In bovine species, expression of IGF type 1 receptor has been reported to increase during the development of primary follicles to antral follicles [39]. Changes in expression of the mentioned growth factors and their receptors indicate that they may play a role in the control of early follicle development.

3. Signaling mechanisms that controls primordial follicle activation and survival

Culture of ovarian cortical tissue has been used to study primordial follicle activation and, in general, most of the primordial follicles start to grow spontaneously after culture in vitro (cow: [91,92]). Initially, it was suggested that an inhibitor of medullary origin regulates activation in vivo and that separation of the cortex from medulla causes bovine primordial follicles to activate in vitro [93]. More recently, Kawamura et al [94] demonstrated that ovarian fragmentation in murine species increases actin polymerization and disrupts Hippo signaling pathway, leading to an increase in the expression of CCN growth factors. The name CCN is derived from major family members including cysteine-rich angiogenic protein (CYR61 or CCN1), connective tissue growth factor (CCN2), and nephroblastoma overexpressed (NOV or CCN3). Secreted connective tissue growth factor and related factors promoted primordial follicle growth in vitro (reviewed by Hsueh et al [29]). In addition, a large number of growth factors and hormones are involved in the activation of primordial follicles (Fig. 1). Among them, FSH (goat: [95]), GDF9 (goat: [96]), BMP15 (goat: [87,97]), IGF1 (goat: [90]), *KITLG* (goat: [85]), BMP7 (goat: [98]), estradiol and progesterone (goat: [99,100]), leukemia inhibitory factor (LIF; goat: [101]), lipopolysaccharides (cow: [102]), melatonin (goat: [103]), growth hormone (goat: [104]), FGF2 (goat: [105]), FGF10 (goat: [106,107]), TGFβ (goat: [108]), and dehydroepiandrosterone (sheep: [109]) promote primordial follicle activation and increase follicle survival (Fig. 1). Except for IGF1 and leukemia inhibitory factor, all those growth factors, as well as EGF (goat: [95], sheep: [110]), activin A (goat: [54]), vascular endothelial growth factor (VEGF, goat: [111]), bone morphogenetic protein 4 (BMP4, sheep: [112]), and VIP (goat: [89]) also increase oocyte growth (Fig. 1). On the other hand, keratinocyte growth factor (KGF, goat: [113] and AMH, cow: [114]) have no effect on follicle activation, whereas BMP6 increases follicle atresia in vitro (goat: [115]).

The intracellular action of growth factors that control the fate of primordial follicles has been reviewed in murine species [29,116,117]. In short, growth factors, like KITLG, activate the phosphatidylinositol 3 kinase (PI3K) pathway in oocytes. The PI3K pathway includes components like serine/threonine kinase (Akt), forkhead transcription factor 3 (FOXO3), glycogen synthase kinase 3A, GSK3B and phosphatase and tensin homolog deleted on chromosome 10 (PTEN) (mice: [118]). FOXO3 is a downstream effector of the PTEN/PI3K/AKT pathway [119]. In mouse ovaries, FOXO3 causes suppression of follicular activation, preserving the follicular reserve pool [120]. A considerable proportion of the signaling mediated by PI3Ks converges at 3-phosphoinositide–dependent protein kinase 1 (PDK1). The PI3K–PDK1 cascade in oocytes regulates ovarian aging

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