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Minireview

Lipid uptake by insect oocytes

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Abstract

Approximately 30–40% of the dry weight of an insect egg consists of lipid, mostly triacylglycerol (TAG). Although this lipid is essential for the energy needed by the developing embryo, little is known about the mechanism that leads to the accumulation of TAG in the insect egg. Insect oocytes can readily synthesize TAG from free fatty acids (FFAs) and glycerol, however, de novo synthesis of FAs by the oocyte is marginal. Hence, FAs have to be imported from the fat body or the diet. Insect hemolymph contains two lipoproteins that transport lipids, lipophorin and vitellogenin. Both are taken up via endocytosis by the oocyte, however, this provides only about 10% of the egg's lipid reserves. The rest is unloaded from circulating lipoprotein particles at the oocyte surface in the form of diacylglycerol (DAG), the major lipid transport form in insects, or as FFA. The mechanism of lipoprotein unloading at the oocyte surface is currently unclear. Possible roles of the lipid transfer particle (LTP), FA transporters, and lipoprotein lipase activity are discussed.

Keywords: Oocytes; Lipid uptake; Lipoprotein lipase; Lipid transfer particle; Fatty acid transport protein; Fatty acid binding protein; Vitellogenin; Lipophorin

1. Introduction

Insect eggs, like eggs of other animals, have to contain all substances necessary for independent development of the embryo. Therefore, in addition to nucleic acids, mature eggs have to contain large amounts of proteins and lipids that can serve as building blocks and as a source of energy. Oocytes synthesize only small amounts of protein. Most proteins are taken up during oocyte development by receptor mediated-endocytosis. The accumulation of protein reserves in insect oocytes is well studied (for reviews see Raikhel and Dhadialla, 1992: Sappington and Raikhel, 1998). Much less is known about the accumulation of lipid reserves.

Lipids, mostly triacylglycerol (TAG), and smaller amounts of phospholipids (PL) and cholesterol, make up 30–40% of the dry weight of the insect oocyte (Allais et al., 1964; Troy et al., 1975; Briegel, 1990; Kawooya and Law, 1988). Lipids are the main source of energy for the developing embryo (Beenakkers et al., 1981). Van Handel (1993) has shown that in the mosquito *Culex quinquefasciatus* approximately 90% of the energy used by the developing embryo originates from lipids. In addition, the embryo needs PL for the formation of membranes.

We have very little information about how lipids accumulate in oocytes. Insect oocytes are able to synthesize TAG using fatty acids (FA) (Lubzens et al., 1981; Ferenz, 1985). However, the ability of oocytes to synthesize FA de novo is very limited. In both, *Manduca sexta* (Kawooya et al., 1988) and *Aedes aegypti* (Ziegler, 1997), the amount of FA synthesized de novo by the follicle in vitro corresponds at most to 1% of the lipid found in the mature egg. That

Abbreviations: ACBP, acyl-coenzyme A binding protein; Acyl-CoA, acyl-coenzyme A; ApoLp-III, apolipophorin-III; CoA, coenzyme A; DAG, diacylglycerol; DAGBP, hypothetical DAG binding protein; DAGTP, hypothetical DAG transport protein; FA, fatty acid; FABP, fatty acid binding protein; FATP, fatty acid transport protein; FFA, free fatty acid; HDLp, high-density lipophorin; LDLp, low-density lipophorin; LPL, lipoprotein lipase; LTP, lipid transfer particle; TAG, triacylglycerol; Vg, vitellogenin; VHDLp, very high-density lipophorin

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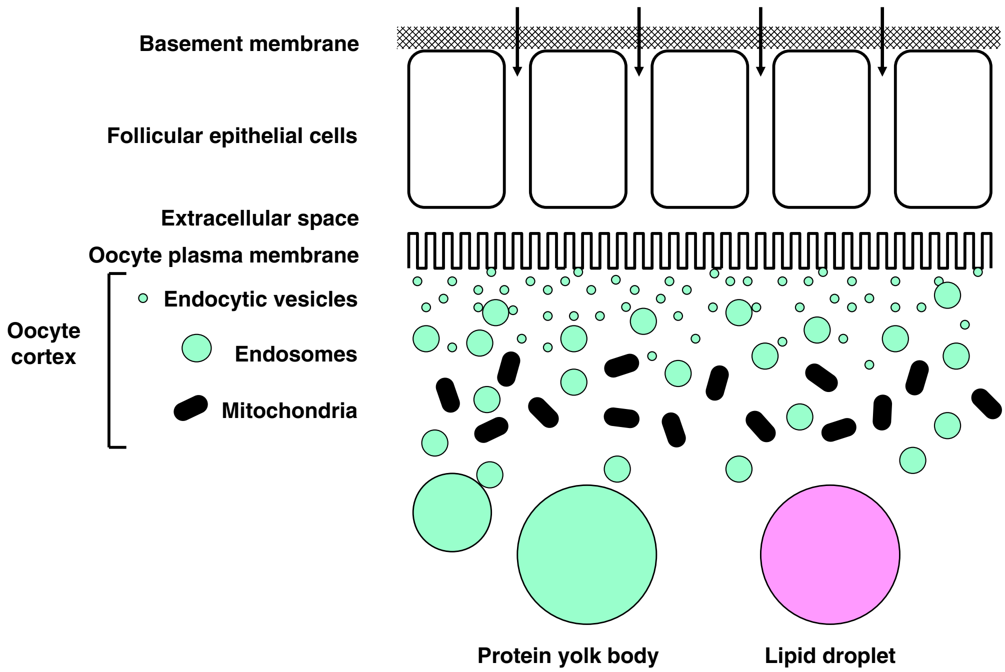

Fig. 1. Subcellular structures involved in the uptake and storage of nutrients by insect oocytes. Hemolymph nutrients cross the basement membrane of the follicle and reach the oocyte surface through the extracellular space that separates the follicular epithelial cells (arrows). Upon reaching the microvillar surface of the oocyte, protein nutrients are taken up by specific receptor-mediated endocytosis. After passing through classic endocytic vesicles and endosomes, these proteins accumulate in spherical protein storage compartments, called yolk bodies. Lipid storage droplets, like mature yolk bodies, are located underneath the oocyte cortex. No specialized structures for the transfer of extracellular lipids to the lipid storage droplets have been identified (after Van Antwerpen et al., 2004).

means nearly all the lipids must be imported. These lipids may originate directly from the diet, or from storage depots in the fat body. The fat body stores lipids that are absorbed from the diet, as well as lipids that are synthesized from carbohydrates (Ziegler and Roth, 1985; Ziegler and Ibrahim, 2001). In the mosquito *A. aegypti* at least 80% of the lipids found in eggs of the first reproductive cycle originate from fat body lipids, synthesized from sugar taken up before a blood meal (Ziegler and Ibrahim, 2001).

In this article, we will review current information on the accumulation of TAG by insect oocytes. We will briefly describe important structural aspects of the ovarian follicle, as well as the composition and function of the lipoproteins which deliver lipids to the developing oocyte. Emphasis will be placed on different mechanisms of lipid delivery that may contribute to the accumulation of lipid reserves in the insect egg.

2. Oocyte structure

Insects have a pair of ovaries, and each ovary consists of several ovarioles. In *M. sexta*, each ovary contains 8 ovarioles with a large number of oocytes, which continuously mature by incorporating lipids and proteins. The number of ovarioles varies in different insects and in some species only the terminal oocytes incorporate lipids and proteins. Each oocyte is surrounded by a sheet of epithelial cells, forming a follicle. Substances to be incorporated into oocytes have to pass the follicular epithelium (Fig. 1). Although vitellogenin (Vg) and the major lipid transporter in hemolymph, lipophorin, are very large molecules, they easily pass through the follicular epithelium to the oocyte. When oocytes mature the follicular epithelium acquires patency (Wyatt and Davey, 1996), that is, the epithelial cells move apart, so even large molecules can easily pass through to the actual oocyte.

Vg is taken up into the oocyte itself by receptor-mediated endocytosis and is processed through the oocyte cortex as endocytic vesicles and endosomes to yolk bodies which are stored deeper in the oocyte. This uptake of proteins appears to be controlled in some insects by a signal from the endocytic follicular epithelium, transmitted by gap junctions (Anderson and Woodruff, 2001). The cortex of the oocytes is rich in mitochondria, this might indicate that the endocytic process uses much energy. Lipids are stored in cytoplasmic lipid droplets, which are located underneath the cortex (Liu and Davies, 1972; Wiemerslage, 1976), deeper in the oocyte, like the yolk bodies (Fig. 1). Lipid droplets contain a TAG core surrounded by a PL monolayer and some proteins and in vertebrates lipid droplets are assembled in the endoplasmic reticulum and then pinched off (Murphy and Vance, 1999; Zweytick et al., 2000). We do not know how lipid droplets are formed in insect oocytes, however, most likely the lipid droplet formation in insects is similar to their formation in vertebrates.