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Peptides in insect oogenesis

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The physiological control of reproduction in insects depends on a combination of environmental and internal cues. In the adult stage, insects become sexually mature and generate gametes. In females, the latter process is designated as oogenesis. Peptides are a versatile class of extracellular signalling molecules that regulate many processes, including oogenesis. At present, the best documented physiological control mechanism of insect oogenesis is the insulin-related peptide signalling pathway. It regulates different stages of the process and provides a functional link between nutritional status and reproduction. Several other peptides have been shown to exert gonadoregulatory activities, but in most cases their exact mode of action still has to be unravelled and their effects on oogenesis could be direct or indirect. Some regulatory peptides, such as the *Drosophila* sex peptide, are being transferred from the male to the female during the mating process.

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Introduction

Peptides constitute a highly diverse class of extracellular signalling molecules which are implicated in the physiological control of many important biological processes, including reproduction. In animals, sexual reproduction is the most common strategy to generate offspring and to allow for rejuvenation and growth of populations. In females, the gametes (eggs or ova) are produced in the ovary via a process that is generally designated as oogenesis. In vertebrates, several peptides and glycoprotein hormones play a crucial role in the neuroendocrine control of reproduction. However, based on the current knowledge, the

situation in insects is less clear and seems less uniform, given the high diversity of species in this largest class of animals. Nevertheless, the success of insects is often ascribed to their high reproductive capacity, in combination with the occurrence of a metamorphosis process that (usually) results in winged adults, which in many cases have different dietary preferences than the larval stages. Insect eggs contain a lot of yolk materials, which serve as nutritional store to support growth and development in the embryonic stage. Therefore, reproduction in insects is dependent on their nutritional and energetic state, as well as on (other) environmental cues. Sexually maturing individuals not only need nutrients and energy to support gonad development and to produce gametes, but they also exhibit energy-demanding activities, such as flight, for foraging, for partner search and for finding a suitable site to deposit their eggs. Therefore, although this review will mainly focus on the current knowledge regarding the control of the oogenesis process by signalling peptides, it is important to keep in mind that this is not a stand-alone process, but is actually situated in a much broader physiological and ecological context. A generalised overview of the known peptides involved in the direct or indirect regulation of oogenesis is given in [Figure 1](#).

The insulin signalling pathway (ISP)

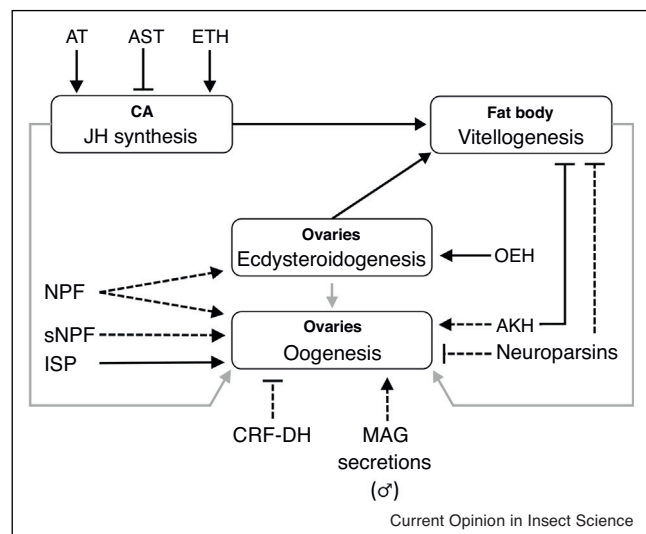
Reproductive processes are functionally linked to the insect's nutritional state. The insulin signalling pathway (ISP) acts as a systemic nutrient sensor, thereby regulating the insect's metabolism in accordance with its nutritional state. For an extensive review on the ISP and its role in reproduction in insects, the reader is referred to [Badisco et al. \[1**\]](#).

In insects, the ISP agonists are designated as 'insulin-related peptides' (IRPs) or 'insulin-like peptides' (ILP) and a different number of paralogs can be found in different taxa, ranging from 1 IRP in locusts [2], over 8 ILPs in the fruit fly [3**], to 30 ILPs in the silk moth [4]. The insulin receptor (IR) is a transmembrane receptor tyrosine kinase, which is capable of activating both the Ras-MAPK (mitogen activated protein kinase) and the PI3K/PKB (phosphatidylinositol-3-kinase/protein kinase B) pathways [1**].

The majority of the available literature on the role of the ISP in oogenesis comes from *Drosophila* research ([Figure 2](#)). For an overview of the oogenesis process in *D. melanogaster*, the reader is referred to [Bellés and Piulachs \[5**\]](#). The ISP is involved in different stages of oogenesis.

2 Development and regulation

Figure 1



General overview of the peptidergic regulation of oogenesis. Different peptides are, directly or indirectly, involved in the regulation of insect oogenesis. This is discussed in more detail in the text. It should be noted that not all interactions are occurring in all insect species. For instance, the stimulation of ecdysteroid synthesis by OEH, and subsequent upregulation of vitellogenesis and therefore the stimulation of oocyte growth, refers to the situation in mosquitoes. Moreover, no neuroparsins have been found in *D. melanogaster*. A dashed line means that the exact mode of action is not known, thus stimulation or repression might result from direct or indirect actions. Juvenile hormones, ecdysteroids and vitellogenins are also involved in the regulation of oogenesis, which is indicated with grey arrows. However, this regulation falls out of the scope of this review. **Abbreviations:** AT, allatotropin; AST, allatostatin; ETH, ecdysis triggering hormone; JH, juvenile hormone; NPF, neuropeptide F; sNPF, short neuropeptide F; ISP, insulin signalling pathway; CRF-DH, corticotropin-releasing factor-like diuretic hormone; MAG, male accessory gland; OEH, ovary ecdysteroidogenic hormone; AKH, adipokinetic hormone.

For instance, both germinal stem cell (GSC) proliferation and maintenance are controlled by dILPs via extension of the G2 and or G1 phase of the GSC cell cycle [6,7,8,9,10]. The extension of the G2 phase goes via the PI3K/PKB pathway, while that of the G1 phase is independent of this pathway [7,8]. The ISP also controls germline growth via the TOR (target of rapamycin) signalling pathway [6,11]. Furthermore, by acting on the cap cells, dILPs promote Notch signalling via FOXO. This Notch signalling is required for cap cell maintenance and as such GSC maintenance [9,10]. A recent study also discovered a FOXO-independent role of the ISP in GSC maintenance, namely via the adipocytes. Activation of the InR in these adipocytes results in the activation of Akt/PKB and the subsequent inhibition of glycogen synthase kinase 3 (GSK3), which eventually results in the maintenance of the GSC [12]. In addition, the ISP is also involved in the control of follicle growth. For instance, dILPs promote changes in the processing body and microtubules of the germ line cells via the TOR signalling

pathway in the follicle cells [13]. The ISP is also involved in the regulation of lipid droplet accumulation in the nutrient-storing germline nurse cells during the final stages of oogenesis. Loss-of-function studies of the tumor suppressor Pten, resulted in the activation of Akt (PKB), which led to the accumulation of lipid droplets in the nurse cells [14]. Later research has shown that this effect was mediated via the TOR pathway [15]. The ISP is also important during late oogenesis, when the mitochondria in mature oocytes enter a low-activity state of respiration quiescence. Sieber *et al.* [17] have shown that a decrease in insulin signalling at the end of the last stage of oogenesis (stage 14) results in respiratory quiescence by remodelling the electron transport chain (ETC). This respiratory quiescence is mediated via GSK3 and results in the accumulation of glycogen, which is required for the developmental competence of the oocyte [16].

The role of the ISP in other insects is less documented. For instance, in the red flour beetle, *Tribolium castaneum*, loss-of-function studies of several components of the ISP have confirmed the crucial role of this pathway in oogenesis. An RNA interference (RNAi) mediated knockdown of InR, TOR or FOXO resulted in impairment of the maturation of the primary oocyte, as well as defective oocyte growth, right after the primary oocytes move to the neck region of the ovariole. RNAi-mediated knockdown of Akt, PI3K, Chico (an insulin receptor substrate) or the serine kinase S6K2 affected only the oocyte growth and not the maturation of the primary oocyte [17]. Also in the desert locust, *Schistocerca gregaria*, the ISP seems to play a role in oogenesis. The RNAi mediated knockdown of the IRP resulted in smaller oocytes, while no significant differences were observed for the vitellogenin transcript levels [18]. Moreover, in the German cockroach, *Blattella germanica*, RNAi-mediated silencing of InR and TOR resulted in reduced juvenile hormone (JH) biosynthesis by the corpora allata and vitellogenin production by the fat body, which in turn affected the oocyte growth [19,20]. On the other hand, RNAi-mediated knockdown of FOXO in starved females resulted in increased JH biosynthesis and vitellogenin production [21]. As such, it can be concluded that nutritional signals activate JH biosynthesis and vitellogenin production via the InR and TOR, thereby indirectly affecting oocyte growth. Furthermore, in the green lacewing, *Chrysopa septempunctata*, injections of bovine insulin promoted the ovarian growth, increased the vitellogenin abundance and improved the reproductive performance [22]. In addition, in the queenless ponerine ant *Diacamma* sp. InR and Akt are expressed in the nurse cells, oocytes and upper germinal regions of reproductiveness females (comparable to the queen in other ants), but not of worker females. This suggests that the ISP is involved in the differentiation between workers and reproductiveness [23]. Eventually, in the yellow fever mosquito, *Aedes aegypti*, ILP3 has been shown to stimulate egg formation after a blood meal [24].

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