INTERACTIONS BETWEEN CORPORA ALLATA, FAT BODY AND OVARY IN INSECT REPRODUCTION: WHICH CONTROLS WHICH?

by

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ABSTRACT

The classical model describing the endocrinology of vitellogenesis involves the juvenile hormone (JH) produced by the corpora allata (CA), which induces the synthesis of vitellogenin (Vg) in the fat body, which is then incorporated into developing oocytes. However, exceptions and special regulatory loops have been reported in different insects, thus leading to a more complicated picture. In spite of the great diversity encountered, it may be possible to reach a unified scheme of the interplay between CA, fat body and the ovary, where homeostasis is accomplished by autoinhibition and short- and long-loop feedback mechanisms.

KEY WORDS: Insect vitellogenesis, corpora allata, fat body, ovary, juvenile hormone, ecdysteroids.

THE CLASSICAL MODEL

With his experiments of parabiosis with the bug Rhodnius prolixus, WIGGLESWORTH discovered the main effects of JH on insect reproduction. In 1936 he demonstrated that the JHs produced by the CA directed vitellogenesis in Rhodnius by inducing the synthesis of Vg in the fat body. Later, it was observed that JH also elicits the opening of intercellular spaces in follicle cells, thus facilitating the incorporation of Vg into the oocyte (Davey, 1981).

Thousands of papers have confirmed that JH directs vitellogenesis in many insect groups, from Zygentoma to all exopterygota studied so far (locusts, crickets, cockroaches, bugs) and also in beetles within the endopterygota (Engelmann, 1983). However, exceptions and special regulatory loops have appeared in different insect orders, thus leading to a rather more complicated picture.

DIVERSITY AND COMPLEXITY

Gonadotrophic hormones

An apparent exception to the classical model appeared in the 70's, when it was discovered that in mosquitoes ecdysteroids originating in the ovary directed the synthesis of Vg in the fat body. JH also seems necessary here, acting both on the ovary and on the fat body, apparently to capacitate them (Hagedorn, 1985).
In higher diptera, both the fat body and the ovary produce yolk proteins (YPs), which seem structurally different from the Vgs of other insects (Bownes, 1990; Wyatt, 1991). Both JH and ecdysteroids are involved in the synthesis of YPs. Results obtained for Drosophila and Musca (Hagedorn, 1985; Agui et al., 1991) suggest that JH may control the synthesis of YP in the ovary, whereas ecdysteroids could control the synthesis of YP in the fat body, although JH also seems necessary in the latter process.

Lepidopterans are a plastic group with respect to the hormonal regulation of vitellogenesis. In species starting this process after adult emergence (like the butterflies Danaus, Nymphalis, Leucania, Heliothis or Pseudaletia) JH directs vitellogenesis. However, in those species which develop oocytes in late larval or in pupal stages (like Bombyx) stimulation with JH would be in conflict with the regulation of metamorphosis, which requires low titres of this hormone. In these lepidopterans, ecdysteroids from the prothoracic gland, and possibly from the ovary, play the role of gonadotrophic hormones (Cusson et al., 1994).

**Regulatory mechanisms**

Neuropeptides have been shown to modulate the production of JH, which can be stimulatory (allotropins) or inhibitory (allatostatins). In the lepidopteran Manduca sexta an allatotropin and an allatostatin have been reported, and a family of structurally different allatostatins has been identified in cockroaches (Tobe et al., 1994; Bellès et al., 1994). In mosquitoes and flies, where Vg production depends on ovarian ecdysteroids, neuropeptides acting on the ovary to stimulate ecdysteroid synthesis (egg development neurosecretory hormones or ovarian ecdysteroidogenic hormones) have been reported (Raikhel, 1992; Kelly, 1994). In those lepidopterans in which vitellogenesis proceeds in pre-imaginal stages and is ecdysteroid-dependent (Bombyx), the ecdysteroids mainly come from the prothoracic gland which, in turn, is stimulated by a prothoracicotropic hormone (Tsuchida et al., 1987). Other brain factors seem directly involved in Vg production. For example, in Locusta a neurohormone from the corpora cardiaca stimulates vitellogenesis in the oocyte independently of JH (Giardie et al., 1992).

The ovary, in turn, plays a crucial role in feedback mechanisms. In mosquitoes, a peptidic factor of ovarian origin (corpora cardiaca stimulating factor, or neurosecretory hormone releasing factor) promotes the release of the ovarian ecdysteroidogenic hormone (Hagedorn, 1985). In Locusta, another ovarian peptide inhibits JH synthesis by CA incubated in vitro (Ferenz & Aden, 1993). In flies and mosquitoes, ovarian oostatic hormones (OSHs) may be involved in feedback mech-