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Site of Action of the Corpus Allatum Hormone at the Cellular Level in *Schistocerca gregaria*

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1. Introduction

A great deal of work has been done on the participation of the corpus allatum hormone (CAH) in the control of yolk deposition in insect oocytes. As yet we know little of the action of this hormone at the cellular level. An approach to this problem was made by investigating the role of this hormone using the accessory reproductive glands of the male desert locust, *Schistocerca gregaria*. Since these glands are organised as simple epithelial structures, and since they produce characteristic exportable secretions; it was thought they would offer a simple test system for elucidating the site of action of the CAH.

2. Methods and Results

The male accessory glands contain abundant and characteristic secretions 8-10 days after reaching the adult stage (at 30 ± 1°C), and this high secretory activity is maintained throughout the adult life (several weeks), although the initial signs of secretory activity may be evident on the third day. This is the very time when the adult corpus allatum begins to renew its own secretory activity, which reaches a maximum level on or about the eighth day (10).

Newly emerged locusts were allatectomised and their accessory glands examined histologically 18 days later: they contained no secretions. If allatectomy was deferred until the sixth day, when the titre of the CAH in the haemolymph was rapidly rising (10), the accessory glands exhibited only a little secretion when they were examined 18 days after the operation. In a further experiment, male locusts were allatectomised 10 days after adult emergence (when the CAH level was at a maximum), and their accessory glands examined 18 days later: the glands contained a considerable amount of secretion, although far less than in the glands of sham-operated locusts of a similar age. If newly emerged males were allatectomised and then corpora allata from mature

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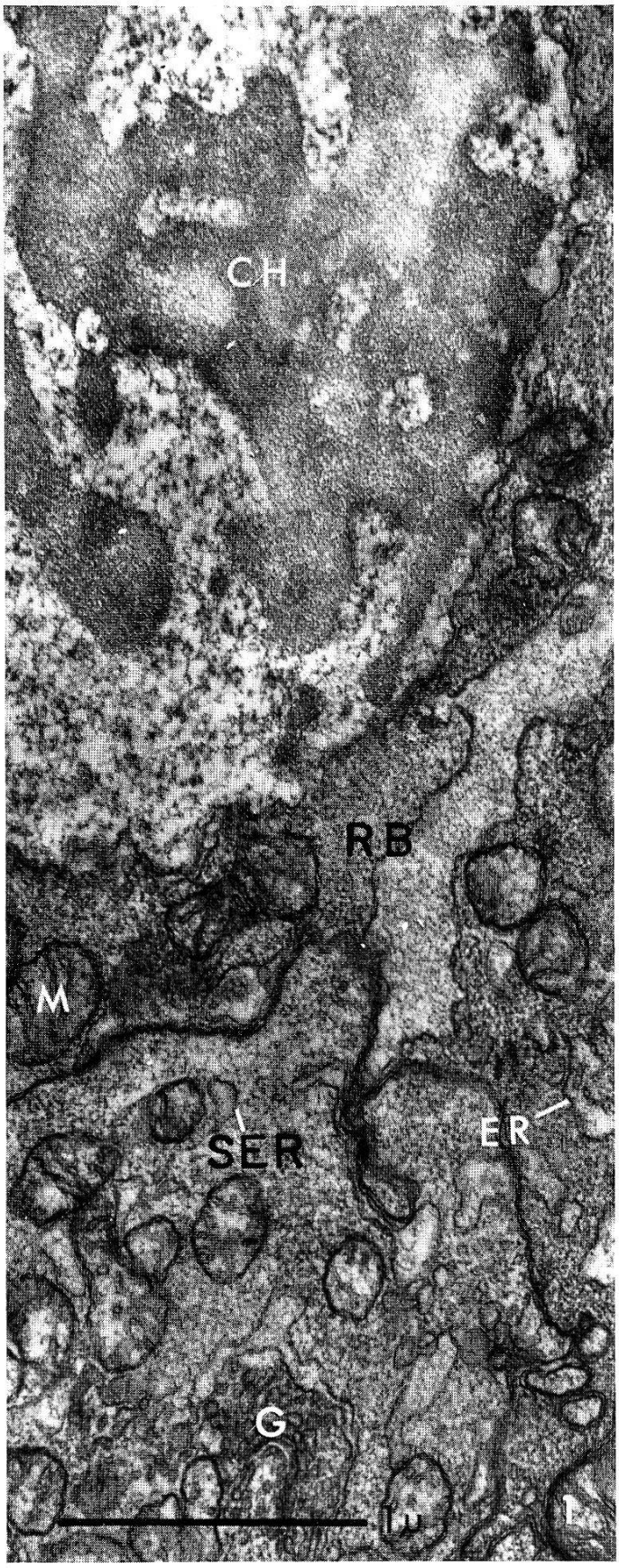

Fig. 1. Electron micrograph of an accessory reproductive gland of a newly emerged adult male locust. The cytoplasm is dominated by free ribosomes (RB). There are few elements of the endoplasmic reticulum (ER), the Golgi apparatus (G) has small "inactive" units, and the mitochondria (M) have simple internal structure. Chromatin material (CH) is clumped. SER = smooth-surfaced endoplasmic reticulum.

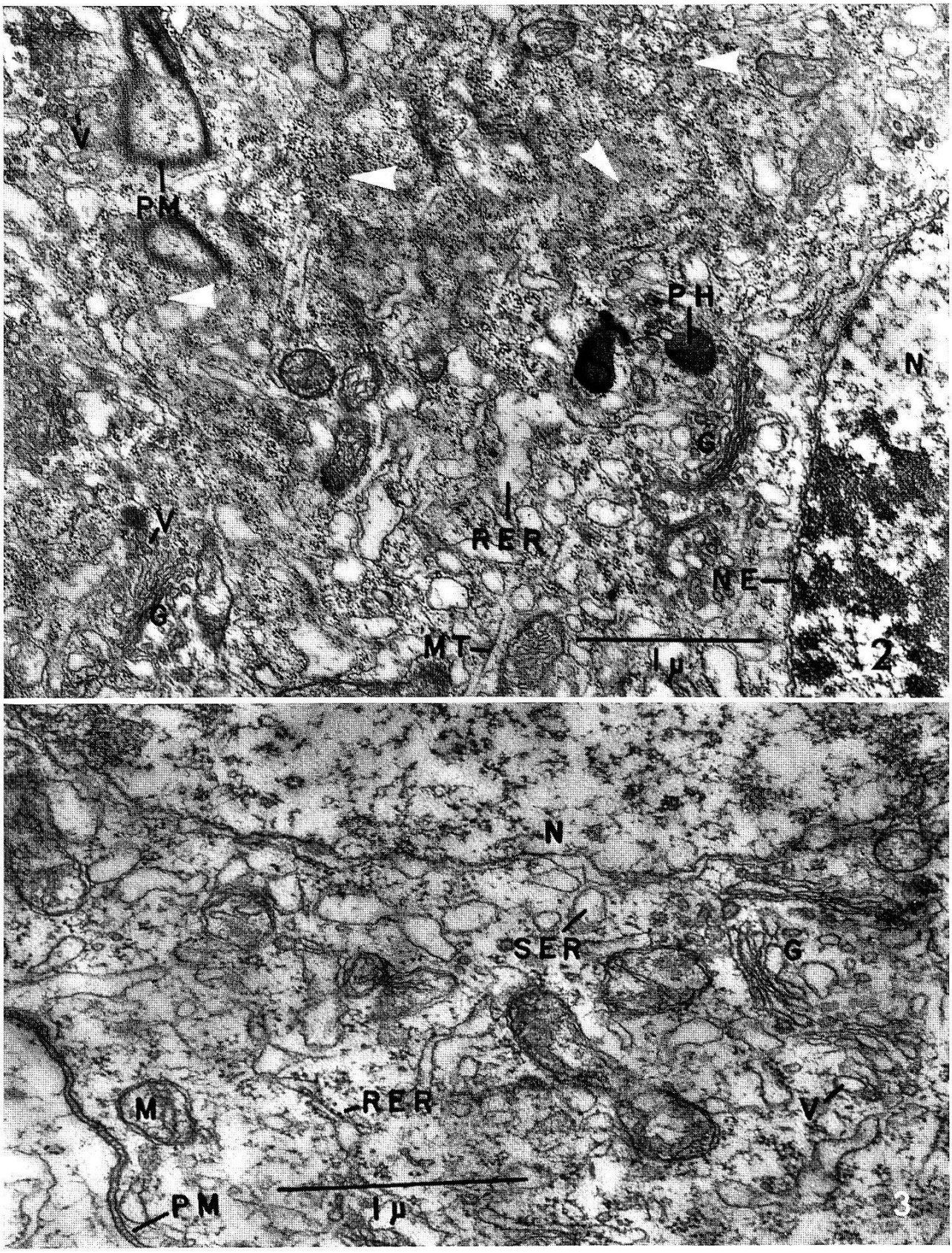

Fig. 2. Electron micrograph of an accessory gland at the start of secretory activity (5 days after adult emergence). The cytoplasm is dominated by the formation of polyribosomes (arrow-heads). Elements of the rough-surfaced endoplasmic reticulum (RER) are common and are often swollen with a fairly electron-transparent content. There are virtually no elements of the smooth-

locusts (9-10 days old) were immediately implanted into the operated locusts, the accessory glands became filled with abundant secretion. It is concluded that the CAH controls the secretory activity of the male accessory reproductive glands of the locust, and that the continued secretory activity of the glands needs the continued presence of the hormone at a high concentration. The regulatory role of the CAH has previously been demonstrated for male accessory glands of a number of insects (7, 17, 20); but it has not been demonstrated in others (1, 6, 12).

Accessory glands from late fifth (i.e. last) instar larvae transplanted into adult locusts having active corpora allata showed mature secretions when examined 18 days later. Accessory glands from early fifth (or earlier) instar larvae similarly treated contained no secretion at all. Thus, larval accessory glands must reach a certain age within the special humoral environment of the fifth larval instar before they can become 'competent' to produce their characteristic secretions. Accessory glands from mature fifth instar larvae transplanted into adult locusts whose corpora allata had been extirpated soon after reaching the adult stage contained no secretions when examined 18 days later. Thus, in the intact animal, accessory glands show no secretory activity during late larval life and early adult life as a result of the absence, or very low titre, of the CAH—although they are competent to produce their characteristic secretions. The development of 'competency' seems to be a problem of metamorphosis or larval differentiation; while the maturation of the accessory glands seems to be the problem of the site and mode of action of the CAH in the special humoral environment of the adult insect.

Observations at the subcellular level have been made with the electron microscope. The accessory glands were fixed for 2 hours in 1% osmium tetroxide in veronal-acetate buffer (pH 7.5) to which sucrose was added, embedded in araldite, and ultra-thin sections double stained in uranyl acetate and lead citrate.

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surfaced endoplasmic reticulum. Golgi complexes (G) are of frequent occurrence and are beginning to enlarge, possessing peripheral vesicles (V) with semi-opaque content. Phagosomes (PH) are sometimes found in the environs of Golgi elements (G). The nucleus (N) shows little blebbing of the nuclear envelope (NE). A superficial section of the lateral plasma membrane (PM) reveals the structure of the septate desmosomes. Cytoplasmic microtubules (MT) are common.

Fig. 3. Electron micrograph of adult accessory gland 12 days after allatectomy. At this stage a normal gland should be fully active; but after allatectomy there is no secretory activity. Most of the endoplasmic reticulum is in the form of smooth-surfaced elements (SER) although rough-surfaced vesicles (RER) do occur. The Golgi complexes (G) are few, and contain few peripheral vesicles (V) and no condensing vacuoles. The lateral plasma membrane (PM) shows septate desmosomes. Other lettering as in Fig. 1.

At the time of adult emergence, the accessory glands of the male locust have acquired at least part of the secretory apparatus —some Golgi complexes, many ribosomes, many mitochondria, etc. But the dominant cytological appearance is one of secretory inactivity: there are no (or very occasionally extremely few) elements of the rough-surfaced endoplasmic reticulum, ribosomes lie free in the cytoplasm, the Golgi elements have no condensing vacuoles, mitochondria are small and of simple structure, and nuclear chromatin is clumped into large masses (Fig. 1). Some or all of these features characterise undifferentiated or embryonic cells in other cell types (11, 15). By the third day, however, significant changes have taken place, chief of which are (a) the first appearance of polyribosomes, especially in the perinuclear region; (b) the organisation of the endoplasmic reticulum into rough-surfaced cisternae; and (c) the enlargement of the Golgi complexes. The chromatin masses are also beginning to be widely dispersed. The whole secretory apparatus is fully functional by the fifth day (Fig. 2).

The notable fact about these changes in the secretory apparatus of the accessory glands is that they parallel changes in the secretory activity of the corpus allatum. This suggested that the CAH may regulate the maturation of the accessory glands by controlling certain events in the nucleus.

To test this idea, newly emerged locusts were allatectomised, and their accessory glands examined 12 days later, when normally the male locust would have reached full sexual maturity (10). It was found that (a) the chromatin masses in the nuclei remained clumped together; (b) polyribosomes were completely, or almost completely, absent from gland cells; (c) the secretory equipment was very largely absent (Fig. 3); but (d) where there was some secretory activity, and it was always infinitesimal, the secretory product was abnormal in structure (which probably reflected its biochemical abnormality). For instance, in cases where the secretory product is normally crystalline in structure, in allatectomised locusts the glands contained a more or less amorphus product.

3. Discussion

The crucial finding after allatectomy is perhaps the lack of polyribosomes—at least this is one of the earliest observable effects. The significance of the polyribosomal structure lies in two recent discoveries (2, 3, 18, 19). First, that the functional units for protein (including enzyme) synthesis are not the single ribosomes but the

clusters of ribosomes (hence 'polyribosomes' or 'polysomes'). Second, that these clusters are held together by a single strand of messenger RNA. The electron-microscopic profiles of the clusters found in accessory gland cells (Fig. 2) are similar to those of biochemically diagnosed polyribosomes (8, 13, 18), in which it has been shown that the amount of a radioactive label incorporated into protein during a very short pulse incubation sediments with the polyribosomes in cell-free extracts, the incorporation being absent in the presence of a very low concentration of ribonuclease (4). Thus, the apparent absence of polyribosomes in the accessory gland cells of allatectomised locusts signifies the possible lack or inactivity of messenger RNA.

One assumption that the new hypothesis implies is that precursor materials enter the accessory glands normally even after allatectomy. That they do so is indicated by the electron-microscopic observation that they possess enormous cytoplasmic bodies (up to 4 μ in diameter) which appear to be phagosomes, which in this case are pinocytotic vesicles that later acquire lysosomal enzymes (9, 14), and which seem to contain unprocessed raw material entering the glands from the haemocoel. If this be so, it shows that precursor materials do enter the glands normally, but that it is the biosynthetic apparatus within the cell that is dormant.

It has been demonstrated above that the CAH controls the secretory activity of the male accessory reproductive glands. That the same hormone also regulates yolk deposition in insect oocytes is well documented (5, 16, 21). Transplantation experiments have revealed that only accessory glands from locust larvae which have passed beyond the mid-stage of the last instar can exhibit secretory activity in an environment of high CAH. Consequently, we have in the adult accessory glands a process of maturation analogous to that found in the developing oocytes, namely vitellogenesis. The inference is obvious: that the hypothesis that has been advanced regarding the site of action of the CAH in the male accessory glands might well have an application to the female gonad.

4. Acknowledgement

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Zusammenfassung

Durch Exstirpation der Corpora allata bei adulten männlichen Heuschrecken verschiedenen Alters konnte gezeigt werden, daß das Hormon des Corpus allatum die sekretorische Tätigkeit der akzessorischen Genitaldrüsen kontrolliert. Die Transplantation akzessorischer Drüsen in adulte Heuschrecken mit aktiver Corpora allata ergab, daß die sekretorische Tätigkeit der akzessorischen Drüsen beginnt, nachdem die Larve die Hälfte des fünften Stadiums erreicht hat, d. h. nach der fünften Häutung. Untersuchungen der Ultrastruktur ließen erkennen, daß das erste Auftreten von Polyribosomen in den akzessorischen Drüsen adulter Heuschrecken zeitlich ungefähr mit dem Beginn der sekretorischen Tätigkeit der Corpora allata zusammenfällt. Nach Allatektomie erscheinen keine Polyribosomen mehr. Deshalb wird vermutet, daß das Corpus allatum-Hormon die Reifung der Drüsen durch Regulieren der Produktion von Messenger RNA kontrolliert.

Résumé

L'extirpation de corpora allata de sauterelles mâles adultes, et d'âges différents, a montré que l'hormone du corpus allatum contrôle l'activité sécrétoire des glandes accessoires génitales. La transplantation de glandes accessoires dans des sauterelles adultes ayant des corpora allata actives ont démontré que les glandes accessoires étaient fonctionnelles après que la larve ait atteint la moitié de son cinquième stade, c'est-à-dire après la cinquième mue. Les polyribosomes apparaissent d'abord dans les glandes accessoires de la sauterelle adulte à peu près au même moment où le corpus allatum commence à montrer une activité sécrétoire. Après allatectomie, les polyribosomes n'apparaissent point. On suggère donc que l'hormone de corpus allatum contrôle la maturation des glandes en réglant la production de messenger ARN.