Hormones in insect behaviour

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Abstract. Hormones play an important role in insect behaviour. These hormones are mainly the neurohormones of the brain and of the corpus cardiacum, the juvenile hormone of the corpus allatum and the ecdysone of the prothoracic glands. These produce either releaser effects or modifier effects. Hormonal modulation of neurophysiological activity controlling various aspects of behaviour, hormonal influence of reproductive behaviour in the male and the female insects, their role in migration, as well as hormonal influence of caste determination and behaviour of social insects, have been discussed.

Keywords. Insect hormones; insect behaviour; insect reproduction; social insects; migration; neurophysiological activity.

1. Introduction

Insects occupy a unique position in the animal kingdom in that hormones are actively involved in the control of behaviour in this group more than in any other group of animals, either invertebrates or vertebrates. This is apparently due, on the one hand, to the rich behavioural repertoire shown by insects and on the other to the accessibility of blood containing the hormones, to the neuronal elements of the nervous system. Ever since the discovery by Bounhiol (1938) that extirpation of the corpus allatum from the penultimate larvae of the silk worm *Bombyx mori* led to precocious, miniature cocoon formation, and especially during the last twenty years there has been a surge of evidence implicating hormonal control of various behavioural aspects in a variety of insect species, like courtship, mating, oviposition, circadian rhythm, autogeny and anautogeny, diapause, caste determination in social insects, feeding behaviour, migration etc. It is in fact preposterous to attempt to cover all aspects of hormonal control of insect behaviour in this brief paper and hence it is intended here to touch upon only a few of the points which are considered rather important.

2. The insect endocrine glands

The insect endocrine system itself consists chiefly of the neurosecretory cells, the corpora cardiaca, corpora allata and the prothoracic glands, of which the latter degenerate during adult metamorphosis and hence are present only in the larval and the pupal instars. In addition, there is considerable mass of evidence implicating ovaries in ecdysone production in many insects though the exact role played by the ovarian ecdysone is far from clear. There are also perivisceral neurohaemal organs associated with the various ventral ganglia (Nayar 1973; Highnam and Hill 1979) whose exact role is known only very little. The neurosecretory cells are scattered in the cerebral ganglia,

but mainly in the pars intercerebralis, distinguishable usually into a median group of "Gomori positive" cells and the lateral group of phloxinophil cells. There may be other groups also. The suboesophageal ganglion and the other ventral ganglia also contain occasional neurosecretory cells. The corpus cardiacum serves as a storage-cum-release centre for the secretory material elaborated in the brain neurosecretory cells; it also elaborates its own hormone. As the brain as well as the cardiacum contain heterogeneous hormones from different sources, removal of these organs resulted in removal of more than one hormonal principle and it was difficult to pinpoint the role of individual hormones until recently when many of these hormones have been isolated and characterized.

3. General effects of hormones on behaviour

The effects of hormones on behaviour have been divided into releaser effects and modifier effects (Truman and Riddiford 1974). Accordingly, a releaser effect of the hormone on behaviour is relatively rapid, and is directly triggered by the hormone. Modifier effect is, on the other hand, slower to appear and results in a change in responsiveness of the nervous system. Hormones may have either only releaser effect, or primer effect or both.

An excellent example of the releaser effect of a hormone is the motor effect to phallic nerve-stimulating hormone, demonstrated by Milburn *et al* (1960) and Milburn and Roeder (1962). It is known that in *Periplaneta americana*, the suboesophageal centres normally inhibit motor activities involved in copulatory movements. Decapitation however removes the sub-oesophageal centre from this inhibition resulting in copulatory movements. When extracts of the corpora cardiaca are injected into male cockroach, it caused rhythmic movements of the abdomen as characteristic during copulation, and when the extract is applied to the nerve cord, evoked rhythmic activity in the phallic nerve. Apparently, the phallic nerve-stimulating hormone acts on the suboesophageal ganglion to remove the inhibition of the motor centres. Though these hormones thus perform the same functions as neural pathways from the brain centres to the lower motor centres, these have the advantage of being sustained in its action, unlike nervous action.

A good illustration for modifier effect of hormone is the effect of juvenile hormone on sexual maturation behaviour. For example, in the female grasshopper *Gomphocerus rufus* (Loher and Huber 1966), juvenile hormone is necessary for development and maintenance of receptivity. The immature female responds to the courting male by primary defence reaction, involving kicking the male and other escape reactions. Corpus allatum induces maturation resulting in copulatory readiness, the female now stridulating and moving towards him, resulting in mounting and copulation. Allatectomy of newly emerged adult female or of sexually mature female results in maintenance in the animal, or its reversion, to defensive behaviour respectively. Primer pheromones bring about secretion of a modifier hormone resulting in a change in behaviour as in the case of maturation pheromone facilitating maturation in male *Schistocerca* by JH release, or long term effects of changing environmental stimuli such as migratory behaviour in *Oncopeltus* under the stimuli of decreasing day length due to juvenile hormone secretion or again, co-ordinating behaviour with developmental or physiological changes of the animal.

4. Hormonal modulation of neurophysiological activity

Neurophysiological basis of hormone action has started receiving attention in recent years. As reported earlier, the effect of the extract of the corpus cardiacum on some of the inhibitory centres in the nervous system of the cockroach which normally repress motor programme resulting in copulation, have been demonstrated neurophysiologically.

Activation of the adult behaviour in wild silk moths is another interesting example. Development and differentiation of the adult nervous system is completed in the wild silk moths (*Antheraea pernyi, A. polyphemus* and in *Hyalophora cecropia*) in the pharate adult even though the pharate adult does not show adult type movement even if the pupal skin is peeled off, before the normal time of eclosion. That its nervous system is comparable to that of the adult is shown by the fact that the peeled pharate male exposed to female sex pheromone under dim illumination shows normal electroantennogram, although it does not show any behavioural response characteristic of the normal adult male, indicating the inhibition to be likely of central nervous nature. This behavioural deficiency of the peeled pupa extends to other aspects of behaviour like lack of tonus, even simple righting reflexes etc. It shows only occasional spasmodic movements of the legs, abdominal twitches and pupal-like rotary movements of the abdomen. However, at the time of the day when eclosion normally occurs, the peeled moth shows pre-eclosion behaviour consisting of a 1·25 hr long programme of abdominal movements, followed by eclosion and spreading of the wings. This switch over to adult behaviour is hormonally controlled. An eclosion hormone is found in the brain and corpus cardiacum of the pharate moth; when homogenates containing this extract is injected into pharate animals, normal eclosion and precocious adult behaviour was observed. At normal eclosion, the eclosion hormone appears in the blood. Its function thus turns on the adult behaviour. The eclosion hormones turns off certain other parts of the nervous system, for example those motor centres which control the dense bands of intersegmental muscles of the abdomen used in eclosion. The motor neurones which supply these muscles become silent shortly after eclosion, thus leading the muscles to degeneration. When eclosion hormone is injected into isolated abdomen of pharate moths, the hormone triggers muscle degeneration, thus turning off the motor neurones to the muscles.

In *Hyalophora cecropia*, the pre-eclosion abdominal movements of the pharate adult consists of three phases with reference to the type and relative frequency of movements (i) a hyperactive period involving mainly abdominal rotations extending to 30 min; (ii) a rather quiescent period of about 30 min; and (iii) a period of hyperactivity involving strong peristaltic waves moving anteriorly along the abdomen. These series of movements begin 10–30 minutes after injection of extracts containing eclosion hormone into pharate moth or into abdomens isolated from pharate moth. Truman and Sokolove (1972) showed that the timing and patterning of these movements are built into the circuitry of the abdominal gangila, by recording the motor output to the inter segmental muscles from the deafferented abdominal nerve cord. This preparation normally showed very low level of firing. On the other hand, addition of eclosion hormone evoked strong and active motor output, beginning 20–40 minutes after addition of hormone. This was followed by a decline and then by new frequent bursting of volleys. The timing and the bursting pattern was such as would result in the pre-eclosion behaviour of the pharate adults, were the efferent fibres connected to the

muscle bundles. The above motor programmes are hence encoded in the abdominal ganglia, and the eclosion hormone activates the programme.

The flashing of the firefly beetle *Luciola* is an example to illustrate a case of peripheral hormone action. Light-induced inhibition of flashing is due to a central mechanism acting on the pacemaker, and a peripheral mechanism acting on the lantern itself. That a hormone produced by the testis is involved in this peripheral inhibition has been shown by connecting the haemocoel of two fire fly beetles and covering the eyes of one partner by opaque paint. When the other partner is illuminated, flashing by the "opaque" partner was also inhibited; when the testis of the illuminated partner is removed, the inhibition of flashing was abolished (Brunelli *et al* 1968). When the light organ was electrically stimulated directly, the intensity of the flashing elicited was not abolished either by decapitation or by denervation of the light organ. On the other hand, if the eyes of a denervated fly were illuminated, the intensity of the electrically induced flashing was inhibited, which however was abolished if testis was removed (Bagnoli *et al* 1970). Transection of the nerve cord anterior to the ganglion which innervates the testis, destroyed the inhibitory response to illumination, whereas electrical stimulation of the nerve to testis led to inhibition of electrically induced lantern flashing. The flash inhibiting substance stored in and released from the testis is noradrenalin (Bagnoli *et al* 1972). The noradrenalin appears to act peripherally, as application of this substance inhibits flashing, but does not affect the size or frequency of efferent volleys coming to the lantern.

5.   Hormonal influence of reproductive behaviour

Hormonal effects on reproductive behaviour are many and varied; there are vast species difference also. On the whole, it may be said that in the male, influence of hormones on reproductive behaviour is either non-existant or unknown in many species; where they exist, these influences are comparatively simple. Many adults like silk moths display full sexual behaviour immediately after emergence and remains so for the rest of their adult life, there being no opportunity for hormones to play any part in the adult life. However, in some males like grasshoppers and locusts the corpora allata are required for the maturation of adult sexual behaviour. Perhaps endocrine control of male sexual behaviour has been best studied in grasshoppers and locusts (Pener 1974). In this group, information appears to be reasonably thorough in *Locusta migratoria migratorioides*, but rather fragmentary in the other species. Pener concludes that the C-cells of the pars intercerebralis completely control the sexual behaviour, their effect being direct and not mediated through the corpus allatum. The C-cells also activate the corpus allatum completely controlling yellow colour, which exert a secondary effect on mating behaviour; the corpus allatum influences the intensity of sexual behaviour, but does not exercise a complete control since their removal does not completely inhibit mating behaviour.

The corpora allata may be controlled by nervous means by the brain; or the allata may be controlled by the pars intercerebralis neurosecretory cells of the brain. In the cockroach, the neurosecretory hormone as reported earlier, elicits abdominal movements acting on the phallic nerves.

In the female, generally speaking the young virgin becomes receptive to male under the influence of juvenile hormone. This has a direct effect on the behaviour of the female toward courting male, as opposed to the indirect effect of JH on sex pheromone

production and thereby attraction of the male. The control may again be nervous or neurosecretory, as in the male. In the wild silk moths, the sexually receptive female, in response to proper environmental stimuli, assumes, calling posture involving protrusion of the last two abdominal segments which expose the pheromone glands permitting pheromone release. This calling behaviour is under the control of the release of corpus cardiacum's calling hormone under the neural influence of the brain. Injection of blood from calling female into virgin in the absence of proper stimuli, induces in them, calling behaviour.

Apparently, under the neurosecretory hormones released by courtship, copulatory behaviour ensues. Generally, mating is followed by termination of male receptivity and the females thus become refractory which may however be in some temporary, whereas in others, permanent. This may be due to a variety of stimuli, like mechanical stimulus, presence of spermatophore in the female bursa copulatrix or due to the sperms themselves, which might secrete a "bursa factor" acting on the central nervous system. As in the mosquito, accessory gland substances of the male, like matrone, may also be involved. These influences may be coupled with neural influences. Refractoriness may also be due to withdrawal of juvenile hormone or due to factors from maturing ovaries. The spermatheca or the bursa of the female may release hormonal factors which may exert their effect through the central nervous or neuroendocrine system of the female.

There is considerable evidence now that pheromone production in insects is under hormonal control in many species. Whereas in some insects the corpus allatum stimulates pheromone secretion, in some the corpus cardiacum is involved in this activity. However, an inhibitory role for juvenile hormone in pheromone production is now emerging from some recent studies. For example, it has been known for a long time that large quantity of juvenile hormone accumulated in the male saturniid moth abdomen. This store of juvenile hormone is now known to be transferred from the accessory gland of the male to the bursa copulatrix of the female during mating (Shirk *et al* 1980). Webster and Carde (1984) propose that in *Platynota stultana* and probably in other similar moths also, this exogenous juvenile hormone transferred in the seminal fluid to the female might be involved in the switch from virgin to mated behaviour in the female. Mating in this species resulted in termination of calling, and gradual reduction of pheromone in the glands comparable to decapitation of virgin females. Mating apparently terminated neural and hormonal stimuli required for pheromone production; exogenous juvenile hormone treatment in virgin females also gave similar results.

Closely connected with pheromone production is pheromone perception; Schafer (1977) and colleagues have demonstrated that the male adults of *Periplaneta* have nearly twice as many olfactory sensillae as female adults; this sexual dimorphism of adult antennal sense organs appeared only during the adult stage. Treatment of terminal instar with JH mimics resulted in supernumerary larvae lacking antennal sexual dimorphism. Inhibitory action of JH prevented the appearance of antennal sexual dimorphism during normal larval development. Adult males with larval antennae produced by bilateral treatment with exogenous juvenile hormone mimic do not respond to the pheromone although they are completely adult in other respects. Electrophysiological studies involving single unit and electroantennogram recording confirm that a portion of the receptors added at the adult ecdysis are sex-attractant receptors, which are not present in the larval or in the adult female antennae in large numbers, and that topical application of JH mimics to male antennae during terminal larval instar inhibits their development.

In the mated female, release of the neurosecretory material appears to take place, resulting in not only myotropic activity leading to oviposition, but to oviposition behaviour as well (Nayar 1958). When ovarian extract or blood from the female during the oviposition is injected into partially gravid mating females, depletion of neurosecretory cells occurred, followed by oviposition. If median neurosecretory cells are implanted into young females lacking mature oocytes in the ovaries, quivering movements of the genital plates, simulating oviposition behaviour, occurred. Further work on ovulation/oviposition has been reported recently by Davey (1984) who found that in *Rhodnius*, ovulation is stimulated by a peptide neurohormone originating from ten large identifiable neurosecretory cells of pars inter-cerebralis. This neurohormone is released in response to feeding and the other in response to mating. The latter has been investigated in detail in this animal. On mating, female *Rhodnius* releases a spermathecal factor, which is only one of the two factors involved in the release of myotropic hormone from the neurosecretory cells, as mating precedes ovulation by some days. A second stimulus, which is provided by the ecdysteroids from the ovary, also appears to be involved. It has been found that injection of ecdysteroids into ovariectomized female results in an increase of myotropic activity of the haemolymph of mated females, but not in virgins. Bursts of action potentials recorded from the corpus cardiacum during ovulation have been associated with the ten pars inter-cerebralis neurosecretory cells, the source of myotropin. Isolated brain retrocerebral complex from mated female have shown the characteristic action potentials *in vitro* under the influence of ecdysterone. Ecdysterone action on the neurosecretory cells appear to be mediated through aminergic neurons of the pars intercerebralis.

6. Hormone in migration

The case of locusts is one of those which has been studied fairly well especially in *Locusta migratoria* and *Schistocerca gregaria*. Young ones (hoppers) reared in isolation, show moderate level of activity; the adults tend to be solitary and do not perform long flights. On the other hand, when crowded, they become highly active, show marching behaviour and oriented locomotion; their adults become gregarious and undertake migration. This difference is subsequently shown to be due to the better developed prothoracic glands in solitary forms. Experiments involving transplantation of prothoracic glands or injection of their extracts have shown that the gregarious hoppers or adults could be converted to solitary individuals (Carlisle and Ellis 1963). Haskell and Moore (1963) have substantiated these findings by demonstrating that ecdysone reversibly reduced the spontaneous motor output from the metathoracic ganglion of adult locusts. On the other hand, the corpus allatum has been shown to stimulate spontaneous locomotor activity as well as sexual activity by a direct action on the nervous system (Odhiambo 1966).

According to Johnson (1969), migration was triggered when ecdysone was absent and JH titre was low. Subsequent rise in JH level brought about cessation of migratory behaviour and onset of oogenesis. Rankin (1974) analysed in detail the causative factors and hormonal control of flight in the milkweed bug *Oncopeltus fasciatus*, using a series of elegant experiments. In this insect, flight is post-teneral and pre-reproductive. It undergoes an adult reproductive diapause in response to short photoperiods making available longer time for flights of greater duration. Long photoperiods on the other

hand afford favourable breeding conditions, and so it undertakes reproductive activity. A skillful manipulation of corpus allatum and ovaries of the animal, and by starvation as well as topical application of JH or by implantation of corpora allata and by combination of some of these experiments, indicated that the corpus allatum can stimulate flight behaviour and the effect can be duplicated by application of juvenile hormone analogue. The flight system may respond to lower titer of juvenile hormone than does the reproductive system. Rankin and Riddiford (1977) subsequently confirmed that JH was the primary hormone responsible for stimulation and co-ordination of migration and reproduction in *Oncopeltus* by JH bioassay and exogenous application of JH to experimental animals. It is to be noted that in *Dysdercus* sp where starvation stimulates flight, and feeding brings about ovarian development, flight muscle degeneration and vitellogenesis are induced by corpus allatum which is activated by feeding and mating (Edwards 1970; Nair and Prabhu 1984a,b) where the situation is opposite to that of *Oncopeltus fasciatus*.

The migratory behaviour of cockchafer beetle *Melolontha melolontha* is character-ized by reversal of the sense of direction of flight in the female (but not in the male) which is closely connected to the maturation of oocytes. Stengel (1974) and his colleagues have shown that the migratory behaviour of this beetle is a good example of neurohormonal regulation of behaviour which depends upon the existence of two types of neurosecretory activity separated in time. During the life above ground, the female adult undergoes two or three ovarian cycles each of which is characterized by oriented migrations which leads her towards feeding areas consisting of the edge of forest, a thicket or an isolated tree, constituting "pre-feeding flight" during which the ovaries are immature; and then back to the egg-laying sites after feeding and mating in the reverse direction, to the fields whence she came, constituting the "oviposition flight" with fully mature ovaries, to lay eggs.

The male, however, upon leaving the soil makes an oriented flight to the forest, but is not capable of reversal in the sense of direction of flight, but moves only in the adjacent feeding area where it feeds and mates. During the reversal flight the corpus allatum releases its hormone, which releases the reversal mechanism for the flight sense and at the same time, blocks oogenesis. The corpus allatum of the pre-oviposition female can release the reversal mechanism even in the male which does not normally reverse the flight direction. The corpus allatum of the pre-oviposition female containing oostatic hormone, if implanted into prefeeding female whose corpus allatum is active in secreting gonadotrophic hormones, is capable of suppressing its activity and blocking oogenesis. So it appears, two hormones secreted by corpus allatum are involved here. Stengel and his colleagues (see Stengel 1974) have also shown that neurosecretory cells of pars intercerebralis secreted the hormone and they are released by the corpora allata.

7. Hormonal control of social behaviour

According to Lüscher (1975), in termites and in the honey bees, the societies use pheromones which influence juvenile hormone production, which in turn influence caste development. However, considerable differences exist in the mode of action of these principles. In termites and honeybees, the development of reproductives is inhibited by the pheromone of the queen. However, the queen substance of the honey bee inhibits the corpora allata whereas the pheromone of the termite reproductives

stimulates the allatum. Hence the stimulation of replacement reproductives in termites, by the honeybee queen substance. It has also to be noted that the termite pheromone acts on the developing larva whereas the queen substance of the bee acts on the adult worker bees. In bees the pheromone produced by the workers acts upon the larvae, whereas in termites the queen pheromone acts on them. In both cases the corpora allata are stimulated to produce more juvenile hormone, causing queen development in bees and inhibiting development of reproductives in termites.

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