Review

Polyphenism in insects and the juvenile hormone

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1. The case of the tobacco horn worm

During the past four decades or so, there has been a growing realization that juvenile hormone (JH) is widely involved in the development of polyphenism in insects. Recently, a significant paper on an experimental study on polyphenism in an insect has been published (Suzuki and Nijhout 2006), and it carried the thesis forward. An outline of and the main inferences from this study have been summarized by Pennisi (2006). Suzuki and Nijhout have chosen to work with the tobacco hornworm (*Manduca sexta*), which is monophenic and produces only green larvae. A related species, tomato hornworm (*Manduca quinquemaculata*) is polyphenic, producing green and black larvae, as well as those with intermediate body colours. The larvae of the latter species are black when developed at 20°C, and green at 28°C.

Suzuki and Nijhout have worked with a black mutant race of *M. sexta*, the larvae of which are black at temperatures between 20°C and 28°C. If the larvae of this race were heat shocked (by exposure to heat for 6 h before apolysis, i.e. the first step in moulting) at the moult between the 4th and the 5th instar, a range of colour variants were produced, ranging from the original black to nearly normal green. Among the larvae obtained in this manner, selection was done along two lines—a monophenic line by selecting black larvae in each generation to obtain the next generation, and a polyphenic line by selection of normal green larvae. In each generation nearly 300 larvae were reared and subjected to heat shock Of these, nearly 60 were then chosen, following the above-mentioned body colour criteria, to get the next generation. A control line was also maintained; these were subjected to heat shock in each generation, and the next generation was reared without any selection. The monophenic line lost its response to heat treatment after about the seventh generation, i.e. heat treatment now led to the production of only black larvae. In the polyphenic line the body colour remained green even at 28°C. In the control line the body colour showed continuous variation between the black colour of the mutant race, and the nearly complete green colour, indicating polygenic control of body colour.

Suzuki and Nijhout performed experiments by applying ligatures both at the neck and at the base of the abdomen in larvae of the monophenic line as well as in those of the polyphenic line. From these experiments it was inferred that secretions from the head had to be available for the body colour to be melanized. The researchers also determined JH titres in the larvae of the two selected lines during the sensitive period, i.e. at the time of heat shock. The titre of JH in the polyphenic line after the heat shock was found to be much higher than in the corresponding situation in the monophenic line. Obviously, it is the JH titre that determines the extent of melanization. Selections in the two lines clearly indicate that genes control the extent of formation and deposition of melanin in the epidermis. Observations in the control line suggest a polygenic control of this process. From this study it may be further inferred that JH acts as a "middle man" between the genome on the one hand and melanin synthesis and deposition on the other.

The study by Suzuki and Nijhout demonstrates that a part of genetic variability may remain masked and unexpressed in the phenotype, but an environmental change may trigger expression of this part of the genome, with consequent polyphenism. The phenomenon may help survival under changed environmental conditions (this is well explained in the case of *M. quinquemaculata* by Pennisi 2006), and, therefore, has been referred to as "genetic accommodation" by Suzuki and Nijhout. As has been inferred above, JH plays the role of a mediator in the development of melanization in *M. sexta* and *M. quinquemaculata*.

Keywords. Caste differentiation; juvenile hormone; melanization; phase differentiation; polyphenism; retournement

Abbreviations used: CA, corpora allata; JH, juvenile hormone; JHE, JH esterase; RH, relative humidity; SPW, solitary population ware.

Suzuki and Nijhout have defined polyphenism as follows: "Polyphenisms are adaptations in which a genome is associated with discrete alternative phenotypes in different environments." Polyphenism could also be defined as the adaptation of a genotype to produce different phenotypes under different environmental conditions. Verma and Kalaichelvan (2004) have considered polyphenism under the broader category of polymorphism. They say, "….in polymorphism the genic mechanism is prominent, but in polyphenism the role of environment is specially pronounced, while the genotype has a less conspicuous role". Polyphenism is seen in social insects, locusts, aphids and many other insects.

Suzuki and Nijhout have cited a number of earlier authors whose work provided the background for their study. It is attempted here to refer to some more studies, the results of which fall in line with the inferences reached by Suzuki and Nijhout.

2. Polyphenism in bruchids

There are several studies on polyphenism in bruchids (Coleoptera, Bruchidae); these include those of Tiwary and Verma (1989a, b, c, d) and George and Verma (1994, 1997, 1999). In *Callosobruchus analis* and *C. maculatus* there are "flightless" forms (referred to as "A" phase by Tiwary and Verma, and also by George and Verma) and "flight" forms (called "B" by Tiwary and Verma; "B", "X" and "Y" by George and Verma). The "flight" forms are highly melanic in body colour, and those in the "flightless" phase are much less so. In both the bruchid species there are also intermediate forms with intermediate states of melanization. Crowding or a high population density in a culture of *C. analis* increases the proportion of melanic forms (Tiwary and Verma 1989c). That crowding has this effect on *C. maculatus* has also been reported by Utida (1965). George and Verma (1999) reared *C. maculatus* in a laboratory in medium-density cultures, some at a high temperature (>40°C) and at high humidity (relative humidity [RH] >90%), and some others at a temperature of 30 ± 2°C and RH of 70–75%. They recorded a significant increase in the proportion of melanic forms under conditions of high temperature and humidity. It is believed that larval crowding in a legume store brings about both rise in temperature as well as in humidity.

Tiwary and Verma (1989c) carried out selection for 10 generations in 3 lines in high-density cultures in favour of the "B" or highly melanic phase, and in 3 lines in favour of the "A" or light-coloured phase. After the 10th generation in each line, the bruchids were left to themselves, without any further attempt at selection. In those cultures in which selection had been done in favour of "B", in the second post-selection generation, all individuals were "B", and in the cultures in which selection was in favour of "A", out of 150 individuals examined, all except two were "A". Hence, as in case of *Manduca sexta* (Suzuki and Nijhout 2006), genetic control of melanization may be inferred. Occurrence of intermediate forms between "A" and "B" phases in a continuous series in an ordinary culture in either of the two bruchid species mentioned above suggests polygenic control of phase determination in them.

Tiwary and Verma (1989b) applied to just eclosed adults of *C. analis* an extract of corpora allata of the cockroach, a JH analogue, and the bruchid's own JH by implantation in the abdomen of the severed heads of several conspecific, well sclerotized adults in different experiments. In all these experiments they recorded a significant increase in the proportion of "A" individuals, as compared to controls, which had received either application of solvents without JH or implants of coxae of legs in place of heads. That in any of these experiments 100% of individuals did not become "A" points to polygenic control of phase determination, and this shows that some individuals do not have the genetic proclivity to respond to an increased titre of JH.

Bruchids and other phytophagous beetles (Phytophaga = Crambycidae + Chrysomelidae + Bruchidae) show polyphenism in another part of their organization. In the phase "B" males of *C. analis* and *C. maculatus,* "retournement" of the aedeagus is anticlockwise, while in "A" males it is clockwise (Tiwary and Verma 1989a; George and Verma 1994). (By "retournement" of the aedeagus is meant rotation of the male intromittent organ or the aedeagus, during development, about its longitudinal axis. In Phytophaga the rotation is through 180°, so that the ventral surface of the organ becomes dorsal and vice versa. "Clockwise" and "anticlockwise" refer to the direction of the rotation, as seen from the caudal end.) (*see* Kumar and Verma 1971, 1980; Verma 1994.) As has been pointed out earlier, experimental studies by Tiwary and Verma (1989b) show that deficiency of JH promotes appearance of the "B" phase, which is characterized both by a high degree of melanization as well as anticlockwise "retournement". Kumar and Verma (1978) found that, if a freshly eclosed adult of the chrysomelid *Aspidomorpha miliaris* is made deficient in JH by putting a ligature between the prothorax and the hinder body 22 h after eclosion from the pupal skin, and the ligature removed 30–32 h after eclosion, anticlockwise "retournement" occurred in all ten cases, while clockwise "retournement" is almost a rule in the species, and anticlockwise turning of the organ is a rarity among field-collected males of this species.

3. Other cases of JH-induced polyphenism

The potential for polyphenism driven by JH should be investigated in other situations. For example, Kovalev (2004) reported that *Zygogramma suturalis*, a chrysomelid, was introduced in northern Caucasus from North America

for biocontrol of the ragweed *Ambrosia artemisiifolia*. The introduced beetle forms a "solitary population wave" (SPW), moving ahead and effectively destroying the weed. As the SPW advances, two remarkable changes take place in the beetles—increasing melanization of body colour, and appearance of flight capacity, though in the home country the beetle is a non-flying species. About development of flying, the author says, "The formation of 'flyers' had only taken place under high population density stress within SPW…..". It has been noted above that high population density in a bruchid culture induces appearance of "flight" and melanized individuals. If the JH level is estimated in the earlier and advanced parts of the SPW, it is likely that further resemblance with polyphenism in bruchids may be demonstrated.

Muraleedharan (2003), in his review paper, pointed out that JH titre is regulated by a balance between its synthesis and degradation, and the degradation is brought about through its ester hydrolysis by the enzyme JH esterase (JHE). He further says that a higher JHE titre suppresses reproduction in the migratory phase of butterflies. That there is suppression of reproduction in the "B" or migratory phase of the stored legume bruchids *C. analis* and *C. maculatus* has been recorded by Tiwary and Verma (1989a) and George and Verma (1994), respectively.

The migratory phase is correlated with lowering of the JH titre, as has been well demonstrated in several insects (Rankin 1978); among these insects are two beetles, *Melolontha melolontha* and *Leptinotarsa decemlineata*.

Chrysolina aurichelcea is a leaf beetle which is brachypterous and flightless. Suzuki (1978) discovered a population of this species in which some individuals were flying. The flying individuals were all females with underdeveloped ovaries (cf. with the situation in *C. maculatus*, in which "flight" or "B" phase females are many more than males in this phase, and they have less well developed ovaries, George and Verma 1994). Suzuki also noted that flying individuals of the leaf beetle had longer and thicker wings, which were pigmented deep red in the basal part. In addition, the author points out, "Intraspecific variations in the hindwing must be strongly correlated with variation in body colour." However, the nature of variations in body colour was not described by him. If the two phases of this leaf beetle, non-flying and flying, are studied from the standpoint of JH concentration, involvement of the hormone in this case of polyphenism is also likely to be found.

Locusts also show polyphenism similar to that of bruchids. Locusts are grasshoppers which, under certain environmental conditions, produce a swarming or migratory phase. Their swarms are formed in limited areas, covered with vegetation, and surrounded by long stretches of arid land. Oases in deserts are such areas, and are favourable for locust swarm formations. When green hoppers of a locust species go on feeding and multiplying in such a breeding area for some time and their population density increases, darkly pigmented and more active hoppers begin to appear. In a certain climatically favourable year their population size increases so much that typical migratory dark pigmented adult locusts are produced, and they leave the breeding area as a swarm.

Joly (1955) was the first to note involvement of the corpora allata (CA), the gland that produces JH, in phase determination in the locust, *Locusta*. He found that implantation of CA from another hopper in the body of a hopper in a crowded culture resulted in changes in the implant-receiving hopper, so that the adult developing from it showed characteristics of the non-swarming phase. These observations were repeated by Staal (1961) who, in addition, found that, if CA were removed in the fourth instar nymph of *Locusta*, dark pigmentation, characteristic of the swarming phase, appeared in the fifth instar. Thus, in this case too, JH is involved in the production of polyphenism.

Applebaum *et al* (1998) point out that JH has only a limited role in locust phase production. They say, "Juvenile hormone modulates cuticular melanization and the rate of reproductive maturation – specifically regulating vitellogenesis at the transcriptional level and nonspecifically stimulating the translational capacity of the locust fat body. Juvenile hormone does not appear to be involved in behaviour phase transition of locusts. Long term treatment of crowded nymphs with the JH analog methoprene does not lessen their gregarious behaviour…". Similar views have been expressed by Breuer *et al* (2003). They say, "Juvenile hormone, without any doubt, induces certain solitarious characteristics, such as green colouration, but is not the primary causal factor." These authors have inferred from some recent studies that the primary factors, which induce production of the gregarious phase are crowding, physical contact among hoppers and release of certain pheromones.

Wirtz (1973) studied caste differentiation in the honeybee larva through histological, electron microscopical and physiological approaches. He found that topical application of JH on three-day-old worker larvae resulted in the development of queen-like features. From this he inferred involvement of JH in caste differentiation in the honeybee. In this context he says, "From topical application experiments…..it can be concluded that the JH acts as a mediator between food and differentiation of characters. It remains to be investigated in what way feeding regulates the functioning of CA."

Ulrich and Rembold (1983) studied maturation of the endocrine system in female honeybee larvae. They noted that polyploidization of CA cells through endomitoses is complete at the beginning of the fifth instar in a queen larva and at the end of the fifth instar in a worker larva. At the end of larval development the CA volume in a queen larva is

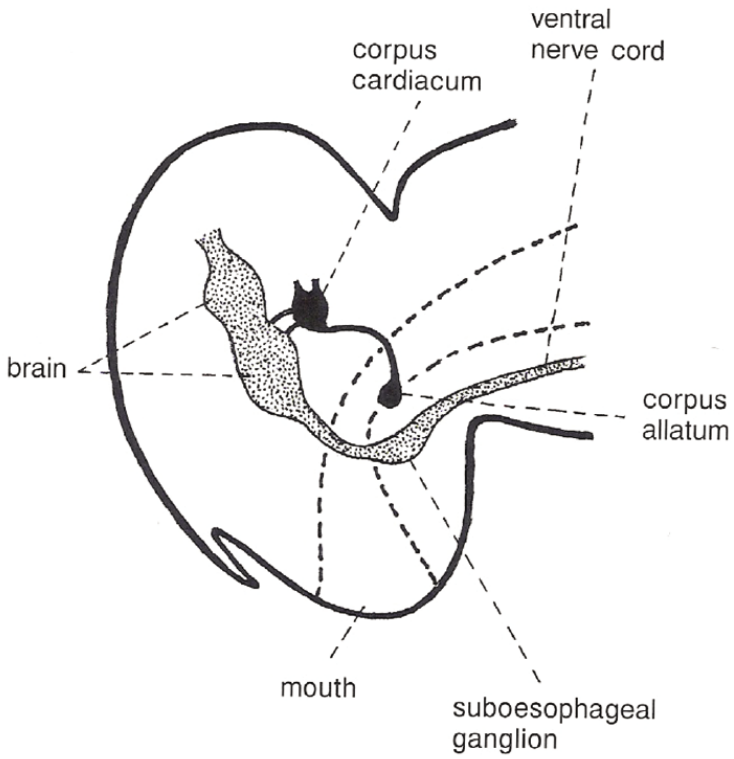

Figure 1. A vertical longitudinal cut through the head of *Locusta* to show the location of corpora allata.

twice that in a worker larva. This is indicative of higher JH activity during differentiation of the queen bee.

Bortolotti *et al* (2001) found that a single application of JH to the first or second instar larva of the bumblebee, *Bombus terrestris*, in a young colony that has just been started by the queen, and in which all larvae are destined to be workers, leads to the thus treated larva developing into a queen. This treatment in older colonies does not produce a clear-cut result, as in such colonies some larvae, without any treatment, develop into queens.

Previous to his monumental work with Suzuki (Suzuki and Nijhout 2006) referred to earlier in this review, Nijhout studied polyphenism in several different insects, in social insects (Wheeler and Nijhout 1981; Wheeler and Nijhout 1983; Wheeler and Nijhout 1984), in the bug *Rhodnius* (Nijhout 1983), seasonal morphs in a butterfly (Nijhout and Rountree 1995; Rountree and Nijhout 1995), and horn length dimorphism in a dung beetle (Emlen and Nijhout 1999). The thesis that JH is involved in insect polyphenism started taking shape in his thinking quite early. Nijhout and Wheeler (1982) said, "It has become evident in recent years that JH is involved in the control of gene switching and that it exerts this control only during certain critical periods," and also, "The presence or absence of JH during any critical period somehow causes the insect to 'choose' between alternative developmental pathways." In this statement, in view of further development in this field of enquiry, "presence or absence of JH" has to be elaborated into "presence or absence of JH or presence of different titres of JH".

After his experience of working on several different polyphenic species, Nijhout says on his website, "We have found that in all these systems [by this he means all the cases of polyphenism studied by him and his co-workers] there are relatively brief critical periods of hormone sensitivity during which the development switch occurs. Interestingly, the hormone sensitive periods of different tissues occur at different times during development…..". The selection experiments by Suzuki and Nijhout (2006) show that in the laboratory (presumably in nature too) change of environs, often with change of habitat, may alter JH concentrations in the hormone-sensitive period, and thus alter the developmental path. As noted earlier in this review, they found the JH titre to be higher in the sensitive period, after the heat shock, in the polyphenic line of selection than in the corresponding period in the monophenic line.

From this review it may be concluded that involvement of JH in the development of polyphenism is widespread among

insects. Whether it is universal among insects cannot be inferred at this stage.

JH is known to be a hormone with multiple effects on the postembryonic development of insects. It seems that initiation of some programmed changes in insects' postembryonic life has become hitched to certain JH concentrations, which may be regulated by sensory perception of certain environmental changes acting through neuroendocrine integration in the region of the corpora cardiaca; hence polyphenism.

We have seen that the extent of melanization of the integument has a relationship with JH titre, and that cases of this relationship are known both among Hemimetabola as well as Holometabola. Hence, the antiquity of the relationship between JH concentration and extent of melanization in insect evolutionary history may be hypothesized.

4. Possible interaction of JH and ecdysteroids in polyphenism development

Though this review is mainly on the role of JH in the development of polyphenism, it would not be out of place to mention briefly here the role of another family of developmental hormones, the ecdysteroids and their possible interaction with JH in producing polyphenism.

Brakefield *et al* (1998) found that, in the butterfly *Bicyclus anynana*, pupae with high ecdysteroid levels develop into adults with large eyespots on their wings, and those with low ecdysteroid levels eclose into adults with small eyespots.

JH has a primary role in the development of horn polymorphism in the scarabaeioid beetle genus *Onthophagus* (Moczek 2006). Emlen and Nijhout (1999) inferred a possible involvement of ecdysteroids in this as well. They measured ecdysteroid titres in male and female larvae and pupae of *Onthophagus taurus*. They observed that the titre showed a rise in the prepupae, both male and female. Several days prior to this rise, a small ecdysteroid peak appears only in female larvae and male larvae that would develop small horns in the adult stage. Moczek (2006) points to a possible role of the steroids too in the production of horn polymorphism in *Onthophagus*.

5. Relation between plasticity and canalization in development

Hatle (2003) pointed out, "Phenotypic variability within a species (the crux of natural selection) can come either from plasticity in development or from genetic variation." Zera and Harshman (2001) suggested that comparative studies on the mechanism of development with plasticity (i.e. leading to polyphenism, involving the role of hormones in gene switching from one developmental pathway to another in a certain critical periods in response to environmental variations) and canalized development (i.e. development under influence of the genotype without any well marked plasticity under environmental influences) are of evolutionary interest. In this context a question that arises is: Has developmental plasticity evolved from canalization? Zhang (2005) says, "The evolved plasticity increases with variances in optimal phenotype and environmental quality; this further induces increases in mean fitness and environmental variance in the trait." This amounts to canalization evolving into plasticity in response to environmental variance.

In order to understand the evolutionary relationship between canalization and plasticity, studies on developmental mechanisms are certainly an interesting area for further research.

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