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The significance of juvenile hormone titers

J. DE WILDE, C. A. D. DE KORT and A. DE LOOF

Hormone circulation

A hormone titer is a steady state regulated by the rates of incrtion and inactivation.

Though hormones exert their function in extremely small dilutions, there is nevertheless a liminal number of "hits" by the messenger required to obtain the response. The effective titer, therefore, is the hormone concentration observed in the direct vicinity of the target organ during induction of the response. In insects, where the hemocoel is a very imperfect "mixing vessel", the hemolymph flows freely in a caudal direction around the visceral organs, fat body and gonads, after having been pushed frontally through the pipeline of the dorsal vessel. Guided by the dorsal and ventral diaphragm, the bloodstream takes a partly laminary, partly turbulent course through cavities of varying diameter and along surfaces of varying texture. It may, therefore, be expected that the blood titer of insect hormones, released by minute localized sources, will not be distributed equally through the hemocoel, and that a blood titer, determined by sampling the total blood of an insect, will represent merely an average value.

For the above reasons, it is not a matter of surprise that corpora allata (implanted in the body cavity) often exert local effects (Joly, 1945; Novak c.s., 1959).

In experiments by de Loof and de Wilde (1970) with allatectomized female Colorado beetles, a local effect was obtained by unilateral injection of juvenile hormone dissolved in paraffin oil. The ovary at the injected side was more activated than the other.

On the other hand, several arguments support a more generalized distribution of hormones through the body cavity. In experiments by Craig and Olson (1951), complete mixing of injected P^{32} occurred in 8–10 minutes in *Tenebrio molitor*, in 25 minutes in *Margantia histrionica* and in 35 minutes in *Anasa tristis*. Although in the intact larvae of fleshflies, ecdysone has a halflife of only 1 hour (Ohtaki c.s., 1968; Karlson and Bode, 1969) and the juvenile hormone is broken down at a similar rate in the adult Colorado beetle (de Kort, 1970) the limited size of insects enables a short circulation time. In *Periplaneta*, this time varies from 3–6 minutes (Coon, 1944), and a given quantity of

hormone can therefore perform 10–20 passages before halflife is reached. The effective titer, therefore, is a function of the circulation time.

This may well be the explanation why in the experiments of Ohtaki c.s. (1968) made with ligatured fleshfly larvae with disturbed circulatory systems, seven times more of ecdysone had to be injected to induce pupation than was ever found in the blood by means of bioassays.

It therefore does not seem necessary to conclude that “the role of the blood is to serve, not as a reservoir, but as a pipeline . . .” (Ohtaki c.s., 1968), and there is still a place for the idea of a regulated titer, be it with a large degree of local variance. This can be corroborated further by the existence of regulatory mechanisms of endocrine activity, and by correlations observed between the blood titer of a hormone and the response of the effector organs.

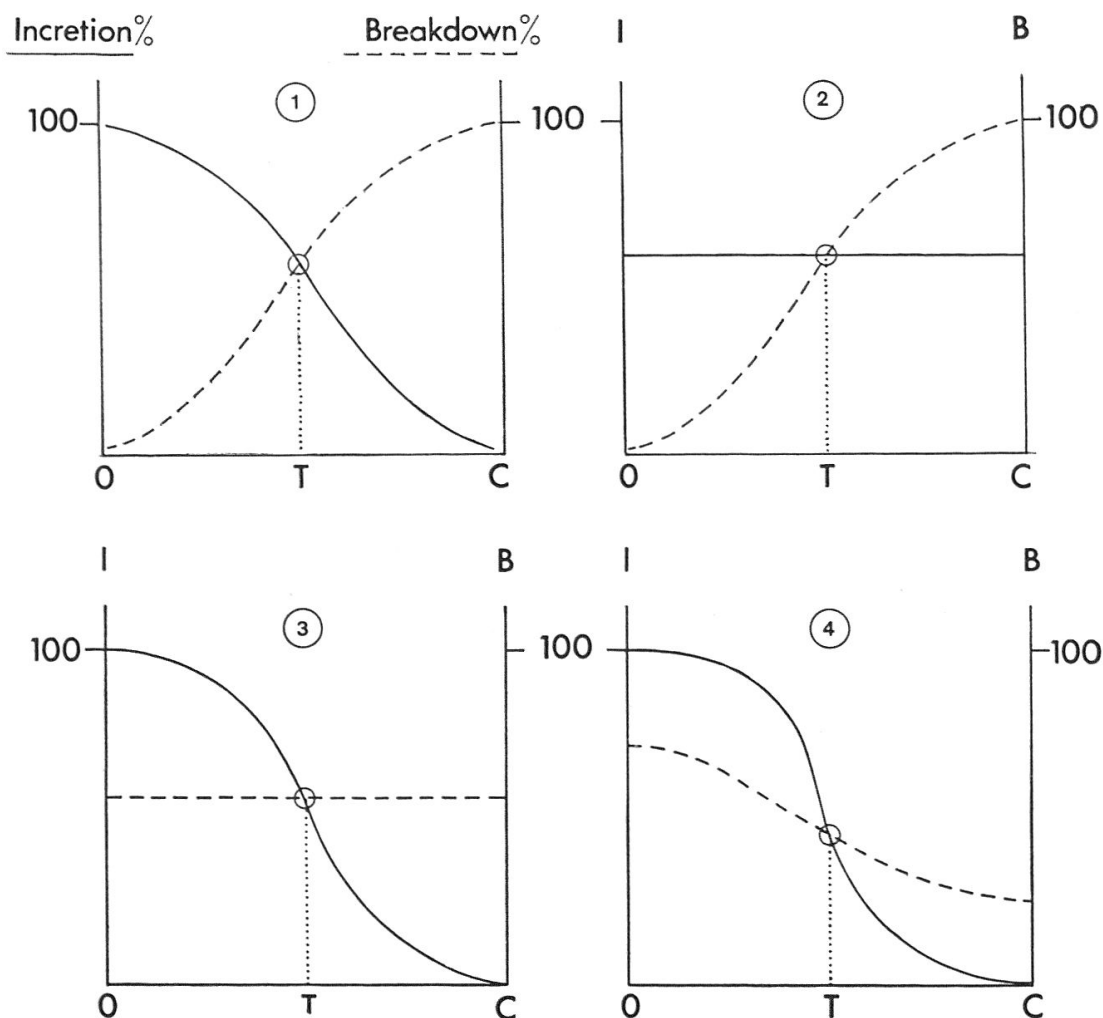


Fig. 1. — Rates of incretion (drawn line) and of inactivation (broken line) in relation to the hormone concentration (c). The titer (T) is regulated by negative feedback, either by both incretion and inactivation rates (1), by inactivation only (2) or incretion only (3). Whenever the inactivation rate follows a positive feedback relation, regulation can only be obtained by a very strong negative feedback on incretion (4).

Endocrine regulation

The necessity of hormone levels to occur at certain critical moments has been apparent from the beginning of insect hormone research. The "critical periods" during the moulting cycles, the periodic endocrine activity in insects with cyclic reproduction (Engelmann, 1968), and the time-dependent effects of hormone levels in locust phase induction (Staal, 1961) would seem to imply a strict regulation of endocrine activity via the brain, either by nervous inhibition or by the constant dominance of its neurosecretory activity. This has been demonstrated in numerous cases for the corpus allatum (de Wilde, 1964; de Wilde and de Boer, 1969), but less so far for the prothoracic gland. In fact it has been recently supposed that the titer of ecdysone in the fleshfly *Calliphora* is chiefly regulated by the rate of inactivation of this hormone by the fat body (Karlson and Bode, 1969).

Regulations of hormone titers generally involve negative feedback systems, of which numerous examples are known in vertebrate endocrinology. Theoretically, both incretion and inactivation of the hormone could be commanded by the "governor", which is either the hormone titer itself or the product of a subordinate organ. Some theoretical examples of this type of negative feedback are shown in Figure 1, 1-3.

Titer-dependent ecdysone inactivation has been suggested to occur in the fleshfly *Calliphora* by Karlson and Bode (1969). Figure 2, derived from the data obtained by these authors, shows that a positive feedback system is proposed. As shown in Figures 1, 4, this can only lead to regulation if accompanied by a highly negative feedback on endocrine input.

Blood titers of Juvenile Hormone

By means of a modification of Schneidermann's *Galleria* waxtest we are now able to measure the blood titer of juvenile hormone in units of 0.000 005 μg (de Wilde c.s., 1968). According to indirect evidence, the activity of the corpora allata greatly diminishes before metamorphosis, and increases again during the reproductive phase of the insect. We were therefore interested in measuring the blood titer of juvenile hormone, especially during these two phases of the life cycle.

a) The prepupal blood titer in *Philosamia cynthia*

Determinations were made during the fourth and fifth larval instar of *Philosamia cynthia*, and during adult life in *Leptinotarsa decemlineata*.

In Figure 3 (after Bartelink, 1969) the data obtained with *Philosamia* are given. Larvae were bled by clipping off a proleg and draining away the blood by means of a pipette. Ether extracts were made from known

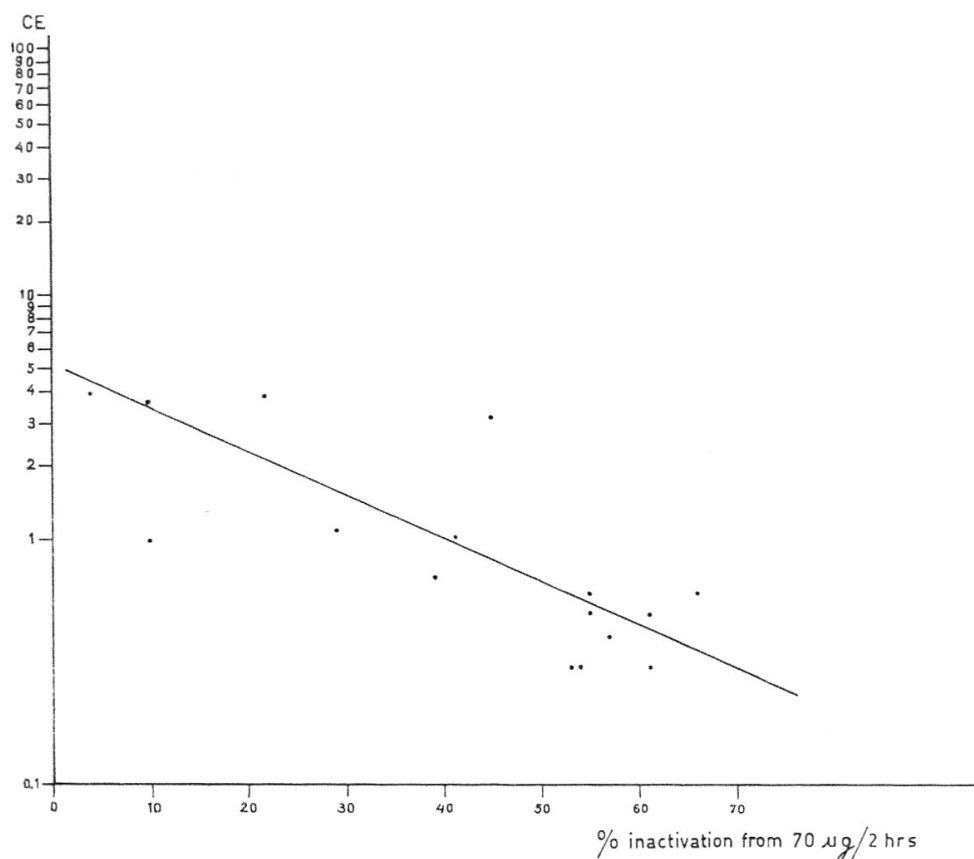


Fig. 2. — The relation between ecdysone titer (in *Calliphora* units, CE) and inactivation rate, according to data obtained by Karlson and Bode (1969), suggests a rather strong positive feedback.

quantities of blood, and, after evaporating the ether, weighed portions of the residue were diluted with equal amounts of olive oil. This dilution was repeated until a dilution end point was reached in the test. Comparison was made with known concentrations of pure juvenile hormone, obtained from Prof. H. Röller *.

It emerges from the graph that a more or less constant high titer of juvenile hormone was observed during the fourth and the beginning of the fifth (last) larval instar of *Philosamia*. Four days after the last larval moult, the titer is lowered to values below the accuracy of the method. This steep decline is well in concert with the conception that the virtual absence of juvenile hormone is a prerequisite to metamorphosis.

b) The blood titer in the adult Colorado beetle female

In Figure 4 the juvenile hormone titer is shown throughout adult

* We thank Professor RÖLLER for a gift of synthetic Juvenile Hormone.

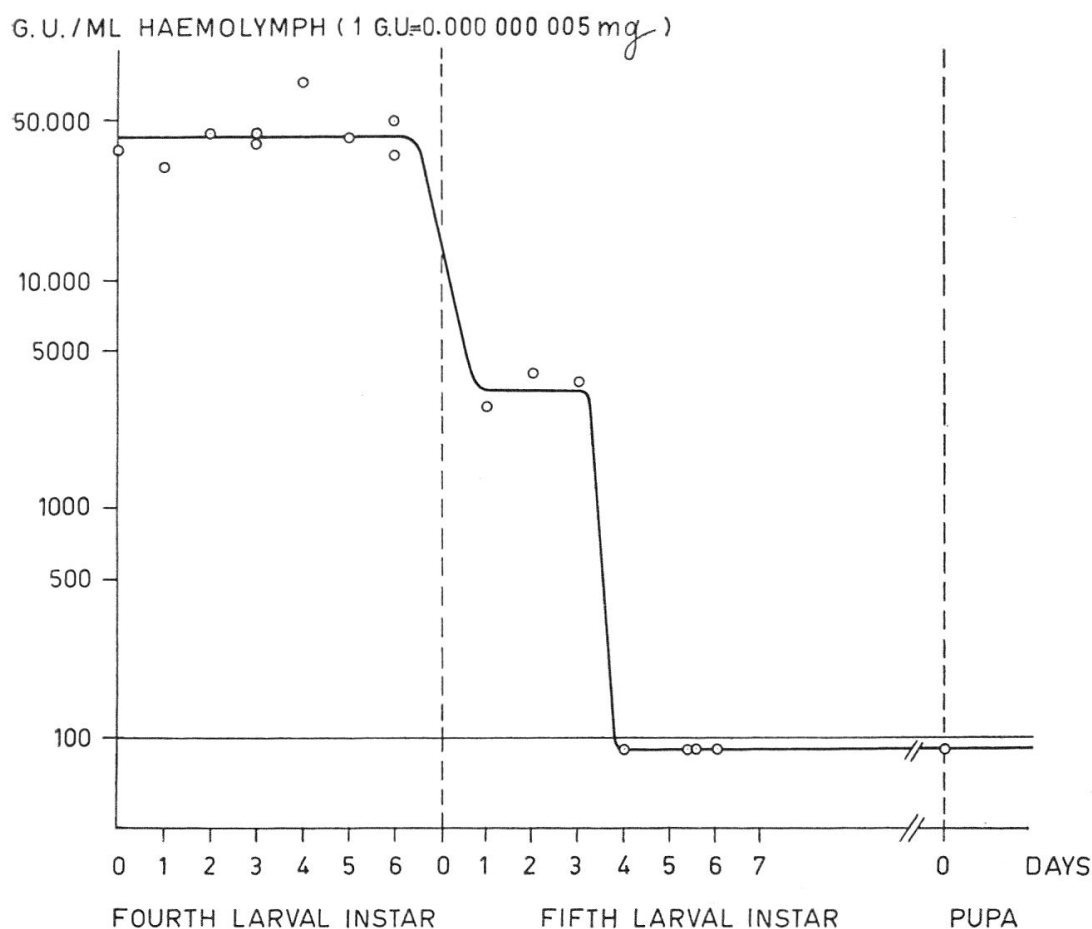


Fig. 3. — The juvenile hormone titer in the hemolymph, during the last two larval instars in *Philosamia cynthia*. Long before pupation, the level is regulated to values below the accuracy of the experiment, and is reduced more than 500 times.

life in *Leptinotarsa* females (de Wilde c.s., 1968). In this beetle, a large number of functions is subordinated to the corpora allata.

1. On the level of the organism : feeding behaviour is induced by high, burrowing behaviour by low levels of corpus allatum activity (de Wilde and de Boer, 1969).

2. On the level of the tissues : Normal vitellogenesis requires high levels, while oosorption can be induced by low levels of corpus allatum activity (de Wilde and de Boer, 1961, 1969 ; de Loof and Lagasse, 1970). Flight muscle development is induced by high, flight muscle degeneration by low levels of corpus allatum activity. (de Kort, 1969).

3. On the subcellular level : repression of the synthesis of "short-day" hemolymph protein and de-repression of the synthesis of vitellogenic female protein are both induced by high levels of juvenile

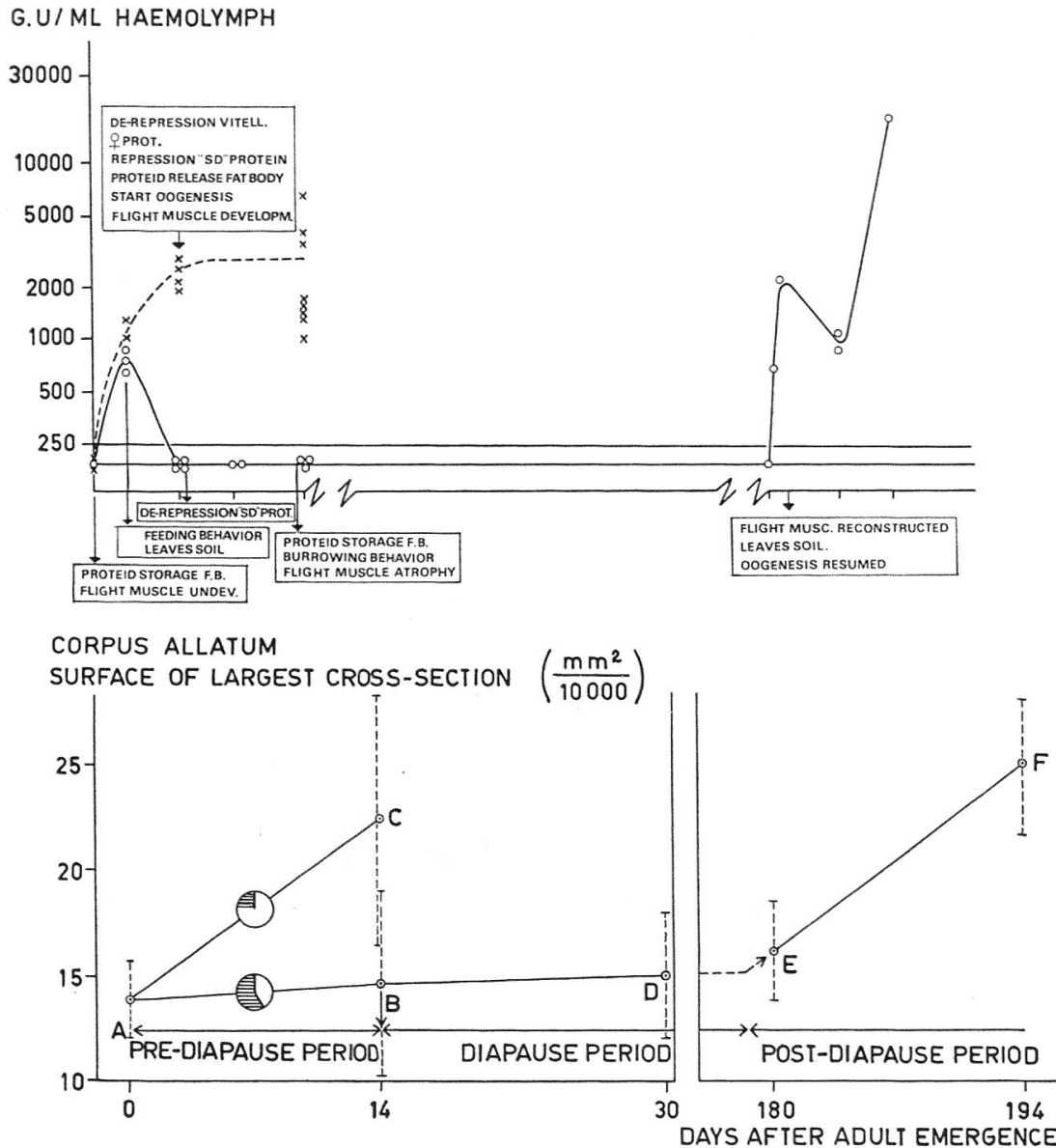


Fig. 4. — Blood titer of JH and corpus allatum size in the adult female *Leptinotarsa*, after de Wilde c.s. (1968). Some physiological phenomena are indicated near the respective hormone titers. Explanation in the text.

hormone (de Loof and de Wilde, 1970). Accumulation of proteid bodies takes place in the fat body cells at low titers of juvenile hormone (de Loof and Lagasse, 1970).

It is a striking fact that, as is shown in Figure 4, during adult life in *Leptinotarsa* several of these features coincide with specifically high or low juvenile hormone titers, and apparently are a function of these titers.

We conclude with some remarks on the "zero titer" of juvenile hormone during adult diapause. In our opinion, it is highly improbable, that a gland showing periodic fluctuations in activity should be completely inactive during any time of its existence. This would imply the full reconstitution of its activity, upon reactivation, and also the periodic removal of its hormone from the negative feedback system.

Much more probable seems a more flowing transition from very low to very high titers, the "thermostat" being set by neuro-endocrine integration.

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