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EFFECT OF JUVENILE HORMONE (III) FROM THE HOST *APIS MELLIFERA* (INSECTA: HYMENOPTERA) ON THE NEUROSECRETION OF THE PARASITIC MITE *VARROA JACOBSONI* (ACARI: MESOSTIGMATA)

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ABSTRACT

Häniel, H., 1986. Effect of juvenile hormone (III) from the host *Apis mellifera* (Insecta: Hymenoptera) on the neurosecretion of the parasitic mite *Varroa jacobsoni* (Acari: Mesostigmata). *Exp. Appl. Acarol.*, 2: 257—271.

In the parasitic bee mite *Varroa jacobsoni* neurosecretory material of ten different cell groups in the synganglion was examined by victoria blue staining after oxidation. Important periods in the life of the mite correspond to definite patterns of filling in of the neurosecretory cell groups. Material of cell group 1, which is situated in the medial protocerebral area of the synganglion, supports molting and oviposition. Secretion of cell group 2, which lies between the two ganglionic masses, seems to be necessary during the whole reproductive process. Cell group 8, located at the opisthosomal ganglion where the genital nerves leave the subesophageal ganglion, seems to be mainly responsible for the initiation of reproduction. Juvenile hormone (JH_{III}) in the hemolymph of the bees acts on the mites as a release mechanism for reproductive behavior with entry into the brood cell of the bee. Mites on bees with a low JH_{III} titer that are sprayed with external JH_{III} show a similar neurosecretion pattern to mites parasitizing bees with a high JH_{III} titer. The influence of external JH_{III} on the degree in which the three cell groups are filled with neurosecretion is discussed with respect to the regulatory mechanisms. In this parasite—host relationship there is a clear synchronization of the reproductive cycle of the mite with the metamorphosis and hormonal regulation of the bee.

INTRODUCTION

Juvenile hormone (JH_{III}) seems to be the most ancient of the arthropod hormones with respect to reproduction (Mordue and Stone, 1979). In the two honey bee species *Apis mellifera* and *Apis cerana*, JH_{III} is the only juvenile hormone. It can be described as the key substance for behavioral changes in the life and reproductive process of bees (Jaycox et al., 1974).

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Varroa jacobsoni is a mite which was found in 1918 in drone cells of *A. cerana*, the tropical honey bee (Buttel-Reepen, 1918). *Varroa* does not reproduce within brood cells of *A. cerana* workers (Koeniger et al., 1981). In this bee species a female mite has to enter a drone cell for successful reproduction. The developmental cycle of the mite is as follows: a female mite enters a brood cell, containing a fourth—fifth stage bee larva, and lies under the larva, within the larval food. After the cell is sealed by other bees the food is consumed by the bee larva and the mite starts to feed on the bee hemolymph in order to develop eggs. This is the start of reproduction. The protonymphs hatch to become deutonymphs, which develop after a final molt into adults. Each female deposits 5—6 eggs, approximately one every day (middle of reproduction). The second egg of each female is usually a male. The adult males copulate within the brood cell with freshly molted females. With the emerging of the bee the inseminated young females and the mother(s) leave the cell (end of reproduction) to parasitize adult bees. Frequently, especially in worker brood cells, mites stay on the larvae and pupae without developing offspring (no reproduction).

Several decades ago *Varroa* came in contact with colonies of *A. mellifera*. In this new host the mite was able to reproduce not only within drone cells but also on worker brood. This leads to an uncontrolled reproduction. In some geographical regions heavy losses of bee colonies were noted because of a quick spread of this mite (Marin, 1978). As *Varroa* can only live on bees and reproduce within bee cells it remained unclear how the mite managed to synchronize its own reproductive cycle with the metamorphosis of the bee within the brood cell.

Some studies on chelicerates (e.g. Chow and Wang, 1974) used the degree to which the neurosecretory cells of the synganglia were filled to investigate the physiological states of single specimens. To our knowledge neurosecretion has not been detected in *Varroa* so far (Ionescu-Varo and Suciu, 1979). A report on the anatomy of the neurosecretory system of *Varroa* will appear elsewhere (Akimov et al., 1986). In earlier experiments we found that a peak in the JH_{III} content of the developing bee larvae serves as a trigger for the start of yolk deposition in the eggs of the mite, which feeds exclusively on hemolymph of bees (Hänel, 1983). Therefore we investigated the filling pattern of neurosecretory cells in the synganglion of *Varroa* at different physiological stages and after treatment with JH_{III}. The question was whether external application of the hormone leads to the same changes in the neurosecretory system as during the parasitization in the brood cell or on adult bees, when the mites feeds on JH-rich hemolymph.

MATERIAL AND METHODS

For the first set of experiments *Apis mellifera carnica* bees, from healthy colonies containing a queen, were checked for parasitizing mites. Brood cells were opened to obtain female *Varroa* in different stages of reproduction.

The mites were fixed in aqueous Bouin fixative for 24 h. With their dorsal shield they were pressed into 1×1 mm areas of slightly melted black beeswax within a wax-covered petri dish. After cooling, the petri dish was filled with 5% formaldehyde. The ventral side of the mite was carefully opened with two fine needles. The synganglion was cleared from adhering tissues and transferred with a paper triangle through the oxidation and staining procedure with victoria blue (Adam and Czihak, 1964). Not all neurosecretory cells which can be detected by using the paraldehydfuchsin-method (PAF) can be stained with victoria blue (Schooneveld, 1970). But we wanted to analyze at least ten synganglia in each group, which would have been too laborious by making serial sections. Bulk staining is, to our knowledge, more difficult and less reliable with methods other than victoria blue. Staining and clearing solutions were filled into glass dishes, which were illuminated from below, to enable the safe transfer of synganglia by floating them on paper triangles. Neurosecretion was followed with dissection binoculars (× 100). For our scoring system we observed the stained synganglia for visible neurosecretion (NS): little NS = a; much NS = b. For each stage and each experimental group different numbers of synganglia were used. The number of *Varroa* synganglia with filled cells and the amount of secretion were recorded.

We are aware of the danger which lies in such a simple score system, but we could not apply optical analyzing devices. The synganglia are rather thick for investigation under a microscope. Therefore we had to use binoculars. Especially the tiny neurosecretory cells at the edges of the synganglia were often hard to see. We chose this bulk staining method to increase the number of individuals investigated. By analyzing the whole synganglia we were able to compare nearly 500 mites. Most of the "cell groups" are formed by only one neurosecretory cell, which was confirmed by serial sections and PAF staining. Previous authors often faced the problem of drawing conclusions from very few serial sections. Severino et al. (1984) carried out representative studies to find correlations between physiological states and neurosecretion, but they partly failed because there was too much variation, although excellent techniques and quantification procedures were employed. Table 1 shows the species of chelicerates in which our neurosecretory cells 1, 2 and 8, among others, have been detected at corresponding areas. It still remains uncertain whether they are homologues or analogues.

In the second group of experiments mites were fixed at different times after hormone treatment. For the JH tests, mites parasitizing adult bees were collected in winter and transferred to two groups of 50—80-day-old winter bees in cages (queenless). The JH titer of such bees is low compared to that of nectar-collecting summer bees (Bühler et al., 1983). Therefore, the bees' natural hormone levels, at that stage, have little influence on *Varroa*. One group of mites was sprayed (Powerpack spraying device) four times at 24-h intervals, each time with 3 ml of acetone:water (1:9 v/v); the other group was treated similarly with the same solvent containing 375 μg JH_{III} (Sigma

Corporation) per 3 ml. The bees were sprayed through the gauze of the cages. Therefore the hormone contacted the mites during spraying and was obtained via the feeding of bee hemolymph. The cages with the parasitized bees were kept under constant, suitable conditions in an incubator. Every day, beginning with the first spraying, ten mites from each hormone-treated and control group were fixed in the same way as in the first set of experiments, to be stained later. All tests were carried out blind. The groups of fixed synganglia received random numbers which were correlated at the beginning and finally after the statistical analysis.

The JH experiment was scored, for example, as follows: in the control group, 78 h after the start of the experiment, ten mites were dissected. In six out of ten mites cell group 1 was equally filled. That makes a score of 60% for group 1 and 40% for group 8 (78 h) (see Table 4).

RESULTS AND DISCUSSION

We found ten distinct victoria-blue-positive neurosecretory cell types in the synganglia of female *Varroa.* The positions of most of them are shown in Fig. 1. Cell group 1 is situated in the cortical layer of the protocerebrum lying close together above the esophagus. Cell group 2 is found between the two ganglionic masses. These cells are further apart than in cell group 1 and lie in the distal part of the brain mass at the inner edge of the cortex, where

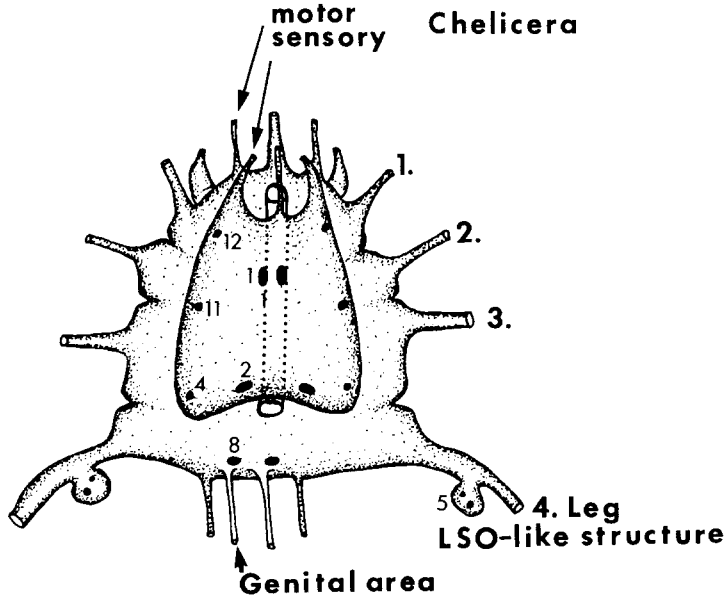

Fig. 1. Synganglion of female *Varroa jacobsoni,* dorsal aspect; numbers with patches indicate the site of neurosecretory cell groups. The LSO-like structure might be similar to the previously described segmental organ and is situated on the fourth leg motor nerve (LSO = lateral segmental organ).

the esophagus leaves the synganglion. Cell group 4 lies a bit distally from group 2; group 5 is situated within a structure at the fourth motoric leg nerve. This structure has a similar histological appearance to the described lateral segmental organ (LSO) in ticks. Figure 2 shows the appearance of this organ in *Varroa* and points out where neurosecretion was found. There is a definite nerve connection of this organ with the genital organs. Cell group 6 is not shown in Fig. 1, for it is situated at the subesophageal part of the synganglion near the center; group 7 lies lateral of group 6. Group 8 can be found on the posterolateral part of the subesophageal ganglion where the genital nerves leave the synganglion. Group 9 lies cranialy, close to the nerves of the chelicerae, group 11 is on the center edge of the protocerebrum, and group 12 lies somewhat more cranial than 11. The cell groups increase in size in the order $1 \geqslant 2 > 8 \geqslant 5 \geqslant 4 > 9 \geqslant 12 \geqslant 11 > 6 \geqslant 7$.

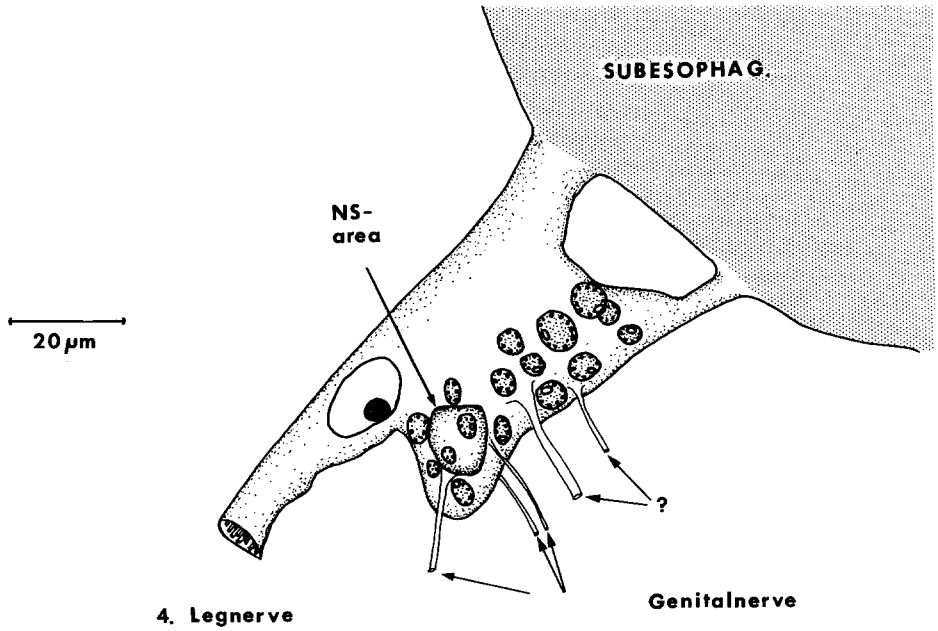

Fig. 2. Line drawning of the presumptive LSO-like organ in *Varroa jacobsoni*, from serial sections (LSO = lateral segmental organ). The nuclei are drawn to show the size of the cells. The neurosecretion (NS) area (paraldehydfuchsin-positive material) is indicated. A comparable structure was found in every female sectioned (n=21).

We tried to compare the position of the detected neurosecretory cell types with the described neurosecretory cells in other chelicerates (Table 1). We did not make any attempt to compare the size and structures because of the different methods used.

Table 2 gives the percentages of mites from each physiological state which showed detectable amounts of victoria-blue-positive material in the different cell types. Particular mention should be made of groups 1, 2, 8 and 12. Cell

TABLE 1

Neurosecretory cells in the synganglion of *Varroa jacobsoni* (victoria-blue-positive cell types) and their putative corresponding cells in other chelicerates

Cell type in *Varroa*	Found in	Reference
1	Araneae	Kühne, 1959
1,12	*Hydrachna* sp.	Streble, 1966
1,2,6,7,8,9,11,12	*Dermanyssus gallinae*	Severino et al., 1984
1,2,4,9,12	*Argas persicus*	Eisen et al., 1973
1,2,7,8,9,11,12	*Ornithodorus moubata*	Eichenberger, 1970
1,2,6,7,8,9,11,12	*Ornithodorus parkeri*	Pound and Oliver, 1982
1,2,8,9,12	*Boophilus microplus*	Binnington and Tatchell, 1973
1,2,7,8,9,11,12	*Dermacentor pictus*	Yoffe, 1965
1,2,9	*Dermacentor variabilis*	Obenchain and Oliver, 1975
1,8,11,12	*Hyalomma dromedarii*	Dhanda, 1967
5,8,9	*Rhipicephalus sanguineus*	Chow and Wang, 1974

TABLE 2

Percantage of individuals of *Varroa jacobsoni* which show detectable amounts of victoria-blue-positive material in the various cell groups during different stages and in the reproductive cycle

Stage	No. of synganglia analyzed (*n*)	Cell type (% of individuals with secretion)									
		1	2	4	5	6	7	8	9	11	12
Deutonymph	15	87a	27a	0	0	13a	0	0	0	0	0
Molting	6	33a	83b	0	33a	33a	0	0	0	17b	0
Copulation	5	0	80b	0	0	0	0	100a	0	0	0
On adult bee	20	46a	36a	4a	11a	0	0	64a	15a	0	0
Start of reprod.	15	93b	33a	7a	0	0	7a	33a	100b	0	0
Middle of reprod.	30	83b	100a	83a	0	13a	0	70b	50b	4a	13a
End of reprod.	28	93b	30a	11a	4a	0	11a	36a	11a	0	46a
No reprod.	15	87a	100b	7a	0	0	0	0	0	0	100b

a = Little neurosecretion; b = much neurosecretion.

group 1: in deutonymphs we find considerable amounts of stored neurosecretory material, which is perhaps released during and after the molt in the adult. During copulation, when the tanning of the cuticle begins, virtually no secretion is detected in the cells. If mites are kept on adult bees in cages, there are only small amounts of secretion, in very few individuals; but when mites at various stages of reproduction inside the brood cell are investigated, they nearly all show detectable quantities. In seven assays, we found secretion in 60 out of 73 synganglia analyzed during reproduction.

Cell group 2: deutonymphs show slight to no secretion, whereas freshly molted specimens and most of the copulating females have very large amounts of stored material. This is absent after copulation. During the parasitizing of adult bees, various amounts of secretion can be found, this partly depends on the age of the bee. During reproduction we found different

patterns of slight filling, but in most cases no heavy storage of material was detectable. The most interesting fact in this cell group was the continuing production and storage of material when no reproduction of the mite occurred within the brood cell. This was the heaviest storage from all observed cell groups and led to a swelling of the cells. An individual with such heavy storage, stained with victoria blue, is shown in Fig. 3. Obviously this neurosecretory material was produced to be utilized during reproduction, but was not released. The reasons for unsuccessful attempts to reproduce are complex. It is an interplay of JH in the bee and, presumably, various other parameters (Hänel and Koeniger, 1986). Cell group 4 seems to be related to the reproduction of the mite, because the filling is restricted to this period. Secretion of groups 5, 6 and 7 is found only rarely.

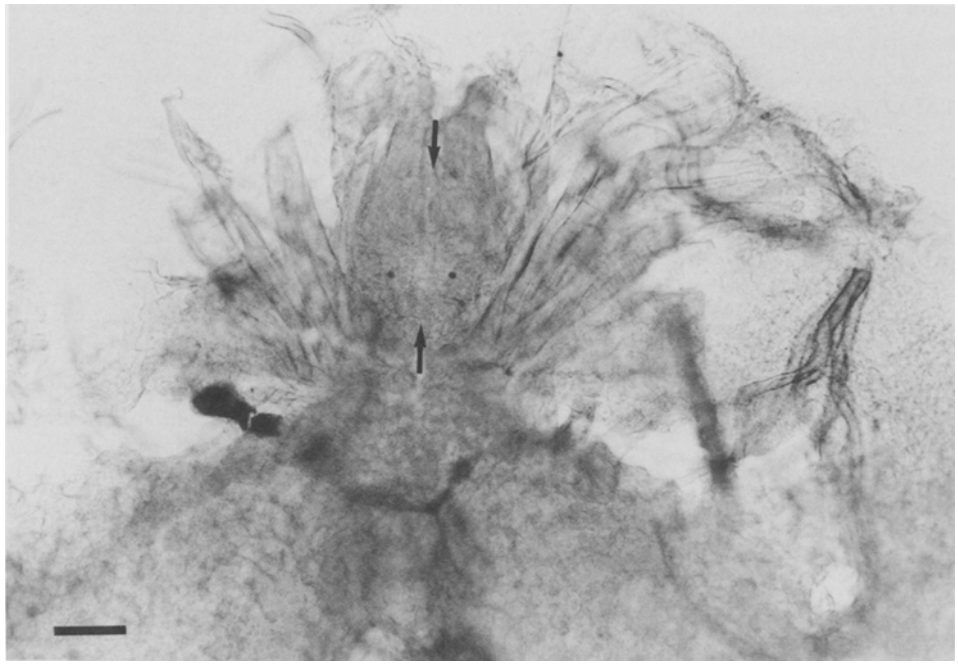

Fig. 3. Victoria blue preparation of a synganglion of *Varroa jacobsoni* (after 7 days in a brood cell without reproduction) showing cell group 2 with heavy storage. Scale bar = 60 μm. The preparation shows a nearly complete female without the cuticle. At the bottom the receptaculum seminis with stained sperm is visible, on the right-hand side some tracheal truncs show up. The esophagus is indicated by two arrows.

Cell group 8 is connected with the genital nerves and shows no secretion in deutonymphs and freshly molted adults, whereas during copulation storage was observed in all the tested mites, but in small quantities only. *Varroa* parasitizing on old summer bees showed heavy storage of secretion, but mites from winter bees had undetectable cells 8, with no neurosecretory

material. This initially produced material was presumably liberated in case of successful reproduction. Perhaps the neurosecretion in group 8 was produced later in connection with oviposition or egg shell formation. This is also indicated by the fact that it was not detectable in cases of an unsuccessful brood cell entry of the mites but, in contrast, was found throughout the reproductive cycle of *Varroa.*

Cell group 9 is filled during the start of reproduction, which might indicate some function in yolk production.

Cell group 12 is filled in case of an unsuccessful cell entry and only shows a little material at the end of a reproductive cycle. This could be part of the information for the mite that the adult bee is about to emerge.

These results are, to some extent, in agreement with the observations of other authors with different chelicerates (Table 3). In Table 3 cell group 8 is seen to be generally linked to the reproductive process, and group 1 seems to take part in molting as well as in reproduction.

TABLE 3

Physiological investigations on the degree of filling of certain neurosecretory cells in different chelicerates which are likely to correspond to neurosecretory cell types 1, 2 and 8 in *Varroa jacobsoni*

Designation of cell	Filling	State	Species	Reference
1	Heavy	Before molt	*Tegenaria*	Kühne, 1959
1	Empty	After molt	*Tegenaria*	Kühne, 1959
1	Heavy	Virgin female	*Dermanyssus*	Severino et al., 1984
1	Empty	Mated female	*Dermanyssus*	Severino et al., 1984
2	Heavy	All females	*Dermanyssus*	Severino et al., 1984
8	Heavy	Before oviposition	*Boophilus*	Binnington and Tatchell, 1973
8	Heavy	Before oviposition	*Rhipicephalus*	Chow and Wang, 1974
8	heavy	Starving	*Rhipicephalus*	Chow and Wang, 1974
8	Empty	After molt	*Rhipicephalus*	Chow and Wang, 1974
8	Empty	After molt	*Hyalomma*	Dhanda, 1967

In the JH experiments the amount of stored neurosecretory material between hormone-treated and control groups was compared every day. In Tables 4 and 5 the results of the synganglion stainings are listed for each single mite. The important cells 1, 2 and 8 are also given in Figs. 4, 5 and 6.

The variation in filling of the other cell types is fairly similar in control and treated groups. Statistical analysis showed that ten mites per group is too small a number to calculate whether there are significant differences between the cell types in groups 4, 5, 6, 9, 11 and 12.

Figure 4 shows the graphs for cell group 1. Initial spraying with JH_{III} released a considerable amount of material, which had disappeared by the time of the second spraying. Thereafter the cells were again filled with neuro-

secretory material and the curves of the JH and control group became similar. In the cage test, where *Varroa* parasitized on adult bees, the mites were not able to enter brood cells. Therefore it is more important to focus on the initial effect of spraying, rather than on the later period. Since the mites could not use the liberated secretion of group 1 in the appropriate way, because of the absence of bee brood, the filling scheme became similar to that of the control group.

Figure 5 shows the analysis for cell group 2. Here it is obvious that there is hardly any effect of the JH spraying on the neurosecretion. The curves are very much alike. This is in agreement with results of the first set of experiments, where cell type 2 was filled in nearly all physiological states.

Figure 6 gives the result for cell group 8. The first spraying with JH_{III} led to the production of large amounts of secretion; this was confirmed in serial sections (stained with PAF). The following JH treatments resulted in a complete release of the material. There was no further significant increase of detectable secretion even after the fourth JH_{III} treatment, 90 h later.

CONCLUSION

We conclude that the material from cell group 1 is needed for molting and perhaps the tanning of the cuticle. As in spiders, we find empty cells at the time of copulation, which is shortly after molting. But there seems to be another function of this type of secretion in *Varroa*. The material is released after the initial spraying with JH. This should be correlated with the initiation of reproduction (see group 8, below). It is produced again even when there is no possibility of entering the brood cells, as in our tests (Fig. 4). A further indication for a function in egg production is the continuous release during reproduction inside the brood cell, observed in the first set of experiments.

We can only guess the function of the heavy storage of material in cell group 2. Tanning of the cuticle or processes in connection with sperm transport or preservation could be considered. The huge amount of secretion stored in the case of an unsuccessful cell entry indicates that the material is always produced during parasitization of bee larvae and pupae. If there is no egg production, the material is obviously not needed and therefore not released. The continuous release during normal reproduction confirms this hypothesis. As JH spraying has virtually no effect (Fig. 5), cell group 2 does not appear to initiate reproduction.

Results from the literature (Table 5) as well as the position of group 8 cells indicate some function of these cells in the reproductive process. This was confirmed by our experiments. We observed that some mites on adult bees with a high JH titer produce large amounts of secretion. This is presumably needed to initiate the act of leaving the adult bee and entering a brood cell for reproduction. The secretion is less detectable at the beginning of parasitization of larvae in the cell. The second pulse of JH from the bee,

Patterns of filling in the neurosecretory cells of individuals of *Varroa jacobsoni* parasitizing on bees; control groups.

Time of parasitization	Cell type								
	1	2	4	5	6	8	9	11	12
16 h	+	+							+
	+	+							+
	+								+
	+						+		+
	+						+		+
	+						+		
	+						+		+
	+						+		+
	+						+		+
	+						+		+
30 h	+	+			+		+		
							+		
	+	+	+	+			+		
	+	+				+			+
	+	+					+		
	+		+						+
	+	+		+					+
	+	+							
	+		+				+		
	+			+					+
54 h	+	+							
	+	+							
	+	+	+	+	+				
	+		+	+	+				
	+		+			+			
	+								+
	+								
	+								
	+		+			+			
	+	+	+				+		+
78 h	+	+							+
		+							+
	+						+	+	
		+				+			+
		+							+
		+				+			
	+	+				+			
	+								+
	+								
	+					+			+

Time of parasitization	Cell type								
	1	2	4	5	6	8	9	11	12
102 h		+				+	+		
	+	+				+			
		+							+
						+			+
		+		+	+				+
		+				+			+
							+		
	+	+				+			
	+	+		+		+			+
	+	+		+			+		+
126 h		+	+			+			
	+	+							
		+				+	+		
	+								
	+	+							
	+		+			+			
	+		+			+	+		
	+					+			
		+	+						
	+	+				+	+		
174 h	+				+				
									+
								+	
		+				+			
218 h	+		+			+		+	
						+			
		+				+	+	+	
		+				+			
						+		+	
						+		+	
		+				+			
								+	
		+							
840 h			+			+			
			+			+			
		+				+			
	+								

TABLE 5

Patterns of filling in the neurosecretory cells of individuals of *Varroa jacobsoni* parasitizing on bees; JH-treated groups

Time of parasitization	Cell type								
	1	2	4	5	6	8	9	11	12
30 h	+		+			+			+
			+			+			+
					+	+			+
	+	+			+	+			+
	+	+		+	+	+			
	+		+			+			+
	+				+	+			+
					+	+	+		+
	+	+			+	+			
	+				+	+			
40 h						+			+
					+	+			
				+	+	+			
					+	+		+	+
						+			+
				+		+			
						+			
				+	+	+			
					+	+			
					+			+	+
54 h	+					+			
						+	+		
		+				+	+		
		+				+	+		
		+				+	+		
			+		+	+			+
	+	+	+		+	+			+
	+				+				
	+	+	+			+			+
	+				+				
78 h	+	+							
	+	+				+			+
	+								+
	+						+		
	+	+					+		
	+						+		
	+								
	+	+					+		+
	+					+			+
	+						+		

Time of parasitization	Cell type								
	1	2	4	5	6	8	9	11	12
102 h								+	
	+	+							
	+				+	+			
	+	+				+	+		
		+							+
	+	+				+			
	+	+							
		+							+
			+						
	+					+			
126 h	+	+	+						
	+	+							
		+						+	
	+	+						+	
	+	+				+			
		+						+	
	+	+					+	+	
	+	+						+	
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		+				+			
174 h				+				+	
			+				+	+	
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218 h					+			+	
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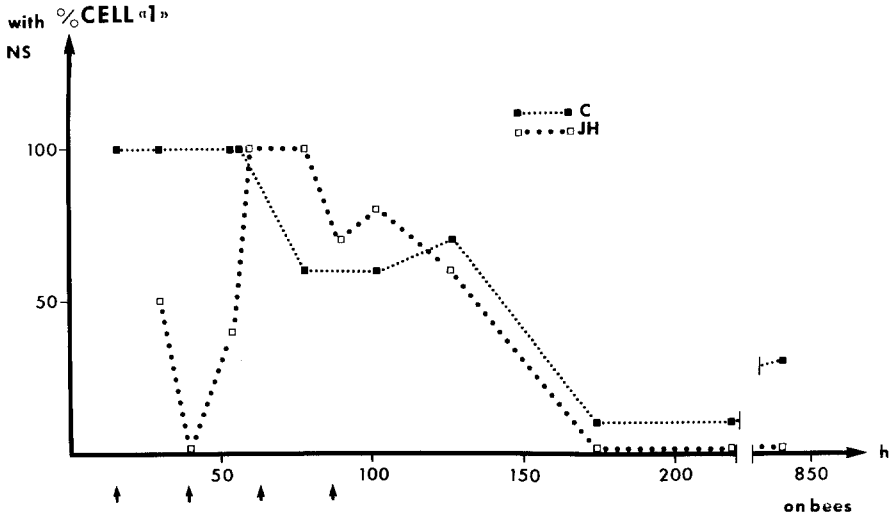

Fig. 4. Neurosecretion of control and JH-treated groups of *Varroa jacobsoni* on bees, cell group 1. Arrows indicate time of spraying; C, control group; JH, hormone group. Each value represents the percentage of synganglia in one group containing detectable amounts of victoria blue positive material (h = hours after start of experiment).

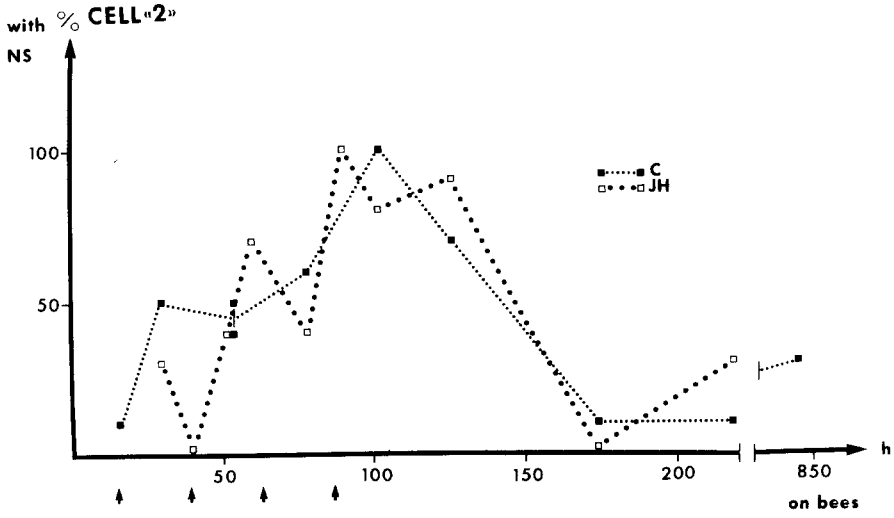

Fig. 5. Neurosecretion of control and JH-treated groups of *Varroa jacobsoni* on bees, cell group 2 (for symbols see Fig. 4).

which takes place on the spinning larvae in the cell (Hänel, 1983), might lead to a quick production and release of material in group 8, which is simulated by the JH treatment, as shown in Fig. 6. The difference between the control groups and the JH-treated mites is obvious during the first days. That means

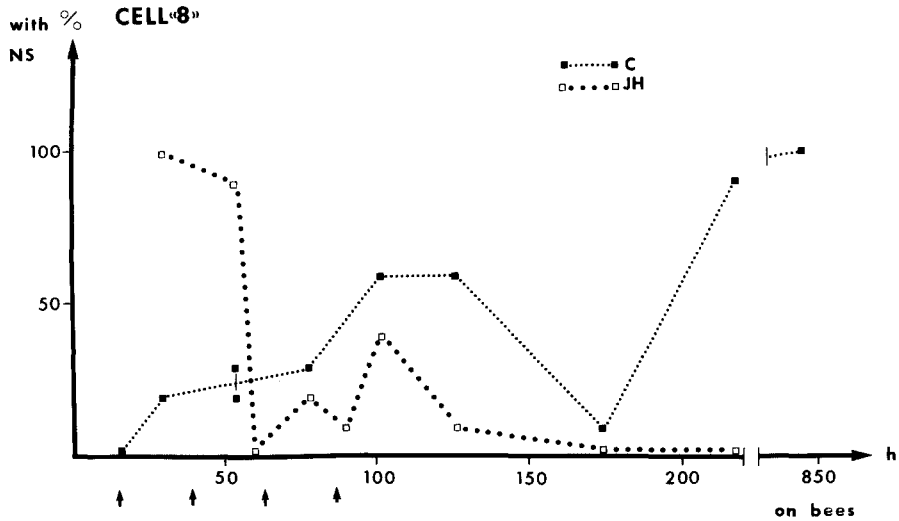

Fig. 6. Neurosecretion of control and JH-treated groups of *Varroa jacobsoni* on bees, cell group 8 (for symbols see Fig. 4).

that secretion of cell group 8 is produced under the influence of the initial JH spraying, which simulates the feeding on hemolymph of larvae containing large amounts of JH or the parasitization of old summer bees, which also have high titers of JH.

In contrast to the material of group 2, protein of cell group 8 is not stored in cases of unsuccessful reproduction but is released and produced in the same way as in group 2 when normal reproduction occurs (Table 2). From this we strongly suspect that cell group 8 functions as one initiator of reproduction in *Varroa*. This initiation phase only lasts for a few days or even less. Some 10 days later the mite is insensitive to external JH. The same explanation could apply for Fig. 5. Even the rising JH titer in bees (after 200—850 h in the incubator) did not evoke any storage of neurosecretion in the JH treated group.

It is exactly these considerations which might lead to a new way of looking for substances to control this serious pest. Hormones, anti-hormones or mimics might interfere with the reproduction of the mite without disturbing the far more sophisticated endocrine system of the holometabolous *Apis mellifera*.

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