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Hormonal Control of Phase Polyphenism in Locusts 【Review article】

飛蝗發育多型性之賀爾蒙調控【綜合論述】

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Abstract

Uvarov (1921) proposed the phase polymorphism theory almost a century ago. Since then much information has accumulated on the mechanisms of outbreaks and phase changes in locusts. In spite of the intensive studies by many pioneer researchers, the hormonal control of phase-related variations in body color and morphological traits remained obscure until recently. Using an albino strain of *Locusta migratoria* as a bioassay system, the dark-color inducing neuropeptides extracted from *L. migratoria* and *Schistocerca gregaria* were determined to be identical to Scham-corazonin. Injection of this neuropeptide not only induces various solitarious body colors but also black and orange coloration characteristically observed in gregarious nymphs of *L. migratoria* irrespective of the rearing density. Furthermore, it has been demonstrated that injection of corazonin causes solitarious locusts to develop morphological characters (body dimensions and antennal sensilla) similar to those observed for gregarious adults in the two locust species. These results suggest that corazonin may play an important role in the control of phase-related characters in locusts.

摘要

將近一世紀前，Uvarov(1921)提出發育多型性理論之後，陸續累積許多有關飛蝗的發育型改變及大發生的機制資訊。雖然經過許多早期學者的戮力研究，但是在荷爾蒙控制的體色及型態變化方面，仍不甚清楚。直到最近利用*Locusta migratoria*白化品系建立的生物檢定系統，從*L. migratoria*及*Schistocerca gregaria*身上萃取出，引起黑體色的神經胜肽和corazonin是相同的。注射corazonin，不但可以引起不同獨居型若蟲體色變化，也能表現出群聚型若蟲體色特有的黑色和梭色（不管飼育的若蟲密度）。並且在獨居型若蟲注射corazonin，會引起型態特徵的改變（體型及觸角的感覺器）與這二種飛蝗的群聚型成蟲相似。這些結果建議corazonin可能在飛蝗發育型相關之特徵調控上，扮演重要角色。

Key words: Corazonin, juvenile hormone, phase polyphenism, locusts

關鍵詞: 黑化誘導激素、青春激素、發育多形性、飛蝗

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Hormonal Control of Phase Polyphenism in Locusts

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ABSTRACT

Uvarov (1921) proposed the phase polymorphism theory almost a century ago. Since then much information has accumulated on the mechanisms of outbreaks and phase changes in locusts. In spite of the intensive studies by many pioneer researchers, the hormonal control of phase-related variations in body color and morphological traits remained obscure until recently. Using an albino strain of *Locusta migratoria* as a bioassay system, the dark-color inducing neuropeptides extracted from *L. migratoria* and *Schistocerca gregaria* were determined to be identical to Scham-corazonin. Injection of this neuropeptide not only induces various solitarious body colors but also black and orange coloration characteristically observed in gregarious nymphs of *L. migratoria* irrespective of the rearing density. Furthermore, it has been demonstrated that injection of corazonin causes solitarious locusts to develop morphological characters (body dimensions and antennal sensilla) similar to those observed for gregarious adults in the two locust species. These results suggest that corazonin may play an important role in the control of phase-related characters in locusts.

Key words: Corazonin, juvenile hormone, phase polyphenism, locusts

Introduction

Locusts are distributed widely in the world. Some locusts are known as the most destructive pest insects because they often form swarms that migrate over long distances. Locust swarms consist of billions of individuals and may cause serious damage to agricultural crops, as described even in the Old Testament. They show density-dependent phase polymorphism, involving graded changes

in morphological, physiological and behavioral traits (Uvarov, 1966, 1977; Fuzeau-Braesch, 1985; Pener, 1991; Pener and Yerushalmi, 1998). Much information accumulated about various aspects of locust biology or acridology in the last century. However, the hormonal mechanism controlling phase polymorphism has not been well understood except for the hormonal control of ovarian development (Dale and Tobe, 1990; Applebaum *et al.*, 1997). Our laboratory started studying

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this subject in 1991 and some findings shed new insights into the physiological mechanisms for the control of phase-related body color and morphological changes in locusts. Here, I will briefly summarize the history of research on this aspect of acridology and describe our findings.

Uvarov and phase polyphenism

Uvarov (1921) proposed the phase polymorphism theory to explain how the locust that had been described as two distinct species, *Locusta migratoria* and *L. danica*, would change from one form to another in response to population density, and suggested that they should be called *L. migratoria*. In his theory, the locusts typically observed at high population density are called gregarious phase and those found at low population density solitary phase. The two phases constitute two extreme forms that show various differences not only in morphology but also in behavior and physiology. At intermediate population density, intermediate forms called transient phase appear. Thus, the variation is continuous in this phenomenon. Numerous studies have been conducted in relation to phase polymorphism (Uvarov, 1966, 1977; Pener, 1991; Pener and Yerushalmi, 1998) and his theory has been widely accepted. Because the term "polymorphism" is often used for genetically controlled variations, the term "polyphenism" is more appropriate to describe environmentally induced variations (Dingle, 1996). Therefore, phase polyphenism instead of phase polymorphism will be used in this paper.

Phase polyphenism has been recognized in several species of locust (Faure, 1932; Uvarov, 1966, 1977). *L. migratoria* and *Schistocerca gregaria* are the most intensively studied species, mainly because of their economic importance. Body color is one of the most conspicuous phase-related traits observed in both species. Solitary nymphs show cryptic body

coloration, whereas gregarious nymphs develop black patterns (Fig. 1), although the black patterns can be induced relatively quickly by crowding even before the locusts attain the gregarious phase. Locusts in different phases show conspicuous differences in body dimensions. Dirsh (1953) discovered convenient morphometric ratios that can be used to evaluate the degree of phase polyphenism: that is F/C and E/F ratios where F=hind femur length, C=maximum head width and E=elytron length. Gregarious locusts have a lower F/C ratio and a higher E/F ratio than solitary ones (Dirsh, 1951, 1953). Locusts in the two phases also show differences in shape of the pronotum (Dirsh, 1953) and numbers of antennal sensilla (Greenwood and Chapman, 1984; Heifetz *et al.*, 1994; Ochieng *et al.*, 1998). Locusts display characteristic changes in behavior in response to population density. Solitary locusts tend to avoid each other, whereas gregarious locusts tend to aggregate. Gregarious nymphs form bands and display a behavior called marching, and adults swarm and often show long-distance migration. The importance of pheromones in locust behavior has been pointed out and their chemical structures and significance were intensively studied in the last decade (Pener and Yerushalmi, 1998; Applebaum and Heifetz, 1999; Ferenz and Seidelmann, 2003).

The role of juvenile hormone (JH)

Joly and Joly (1954) demonstrated that implantation of extra corpora allata induced a green body color in gregarious (crowd-reared) nymphs of *L. migratoria*, indicating that JH produced by the gland is responsible for the induction of green color. Removal of the corpora allata from solitary green nymphs caused the green color to fade away, but failed to induce the expression of black and orange coloration typical for gregarious forms in those individuals, and the involvement of

another factor(s) triggering the expression of gregarious body coloration was pointed out (Pener *et al.*, 1992), although the mechanism inducing the gregarious coloration remained unknown.

Studies on the dark-color inducing factors

A steroid factor in the hemolymph was suggested by Nickerson (1956) as a dark-color inducing substance in gregarious nymphs of *S. gregaria*. He injected hemolymph taken from gregarious nymphs into solitary individuals and observed increased black patterns in those individuals. Staal (1961) examined the effects of organ implantation on various phase-related traits and found that nymphs of *L. migratoria* implanted with extra corpora cardiaca (CC) increased the black patterns, whereas surgical removal of CC produced an opposite effect. Girardie and Cazal (1965) observed that the dark body color became lighter when the lateral cells of protocerebrum were selectively destroyed in the gregarious nymphs. Although these studies strongly indicated the presence of dark-color inducing factors in locusts, their chemical identity remained undetermined. Besides the black patterns and green color, locusts develop other dark colors such as yellow, brown, beige, orange, reddish and black (Fig. 1). However, little information was available about the hormonal factor(s) responsible for the induction of these colors.

Discovery of an albino mutant deficient in the dark-color inducing hormone

Albinism occurs in various groups of animals (Halls, 2004). Locusts are not exceptions (Hunter-Jones, 1957; Pener, 1965; Verdier, 1965). We established an albino strain of *L. migratoria* by selecting albino mutants that had appeared

spontaneously in a laboratory stock originally derived from Okinawa, Japan. The albinism in this strain is controlled by a simple Mendelian unit (Hasegawa and Tanaka, 1994). We found that this albino strain lacks a dark-color inducing factor that is normally present in the brain, CC and thoracic ganglia of this species: implantation of the organs taken from normal (pigmented) nymphs into albino nymphs caused some of the latter to turn gray, reddish, brown or dark brown like the colors of normal solitary individuals, and others to develop black and orange coloration like that of normal gregarious hoppers (Tanaka, 1993). Using the same technique, a factor inducing dark color in the albino *L. migratoria* was also found to be present in the CC of *S. gregaria* (Tanaka and Yagi, 1997) and *Gastrimargus marmoratus* (Tanaka, 2000c). The partial characterization revealed that the CC factors in those species were peptidic substances because their dark-color inducing activity was retained after heating, but lost after incubation with a protease (Tanaka and Pener, 1994a, 1994b; Tanaka and Yagi, 1997).

Isolation of the dark-color inducing factors

We made methanol extracts of CC from normal *L. migratoria* and *S. gregaria* to determine the primary structures of the dark-color inducing neuropeptides using the albino bioassay developed by Tanaka and Pener (1994a). As a result, the two neuropeptides extracted from these locusts were found to be identical to Scham-corazonin or [His⁷]-corazonin (Fig. 2; Tawfik *et al.*, 1999) that had been isolated previously from the American grasshopper, *Shistocerca americana* by Veenstra (1991) without known function.

The presence of corazonin-like factors in other insects was indicated by the albino

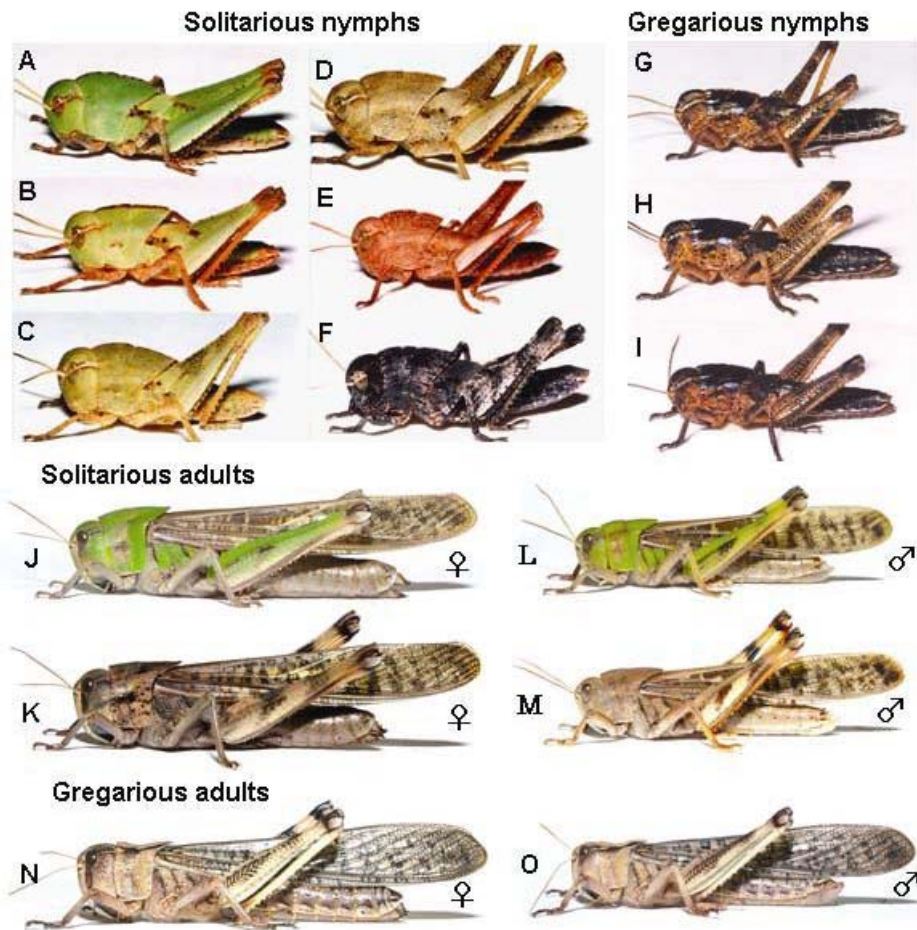


Fig. 1. Body coloration of solitary (A-F, J-M) and gregarious (G-I, N-O) individuals of *L. migratoria*.



[His⁷]-corazonin MW=1,351.6

pGlu-Thr-Phe-Gln-Tyr-Ser-His-Gly-Trp-Thr-Asn-amide

Fig. 2. The amino acid sequence of Scham-corazonin and albino nymphs of *L. migratoria*. The right individual was injected with Scham-corazonin in the previous stadium.

bioassay (Tanaka, 1993; 1996): implantation of brain or CC from crickets (*Gryllus bimaculatus*, *Teleogryllus occipitalis* and *Medicogryllus confirmatus*) and moths (*Spodoptera separata*, *Bombyx mori* and *Cephanodes hylas*) caused darkening in albino locusts. Since then, many species have been screened and the presence of corazonin or similar substances has been indicated for 18 insect orders including pterygote and apterygote insects (Tanaka, 2000c, 2001, unpublished; Roller *et al.*, 2003). The CC of *G. bimaculatus* induced the black patterns in green solitary nymphs of normal *S. gregaria* when implanted (Tanaka and Yagi, 1997). We attempted to characterize the chemical nature of the factors from *G. bimaculatus* and *B. mori* and found a corazonin homolog, Peram-corazonin or [Arg⁷]-corazonin (Hua *et al.*, 2000). This homolog was first isolated from a cockroach, *Periplaneta americana* as the most potent cardiostimulatory peptide (Veenstra, 1989). It is as potent as Scham-corazonin in terms of the dark-color inducing activity in locusts (Hua *et al.*, 2000), but neither of them is involved in the control of pigmentation in those non-locust insects. In *B. mori*, both corazonin homologs affect the silk spinning activity when injected (Tanaka *et al.*, 2002b). Recently, the presence of a third corazonin, [Thr⁴, His⁷]-corazonin, that induces dark color in *L. migratoria* when injected, was suggested for a bee, *Apis mellifera* (Y. Tanaka, L. Roller and S. Tanaka, unpublished).

Antisera against Scham-corazonin were developed to observe the distribution of immunoreactive cells in the central nervous system of locusts. As expected from the results of implantation experiments in previous studies (Tanaka, 1993; Tanaka and Pener, 1994a), strong immunoreactivity was detected in the brain, CC and thoracic ganglia in normal individuals of *L. migratoria* (Fig. 3) but not in albino ones (Schoofs *et al.*, 2000; Baggerman *et al.*, 2001; Roller *et al.*, 2003).

The role of corazonin in the control of body color

The nymphs of *L. migratoria* at low density (solitary forms) show cryptic coloration, either green or different yellow, brown, reddish or black colors, whereas those at high density (gregarious forms) show black patterns with an orange background color (Fig. 1; Faure, 1932; Staal, 1961; Fuzeau-Braesch, 1985; Pener, 1991). In solitary nymphs, the body color depends on various environmental factors including humidity, habitat background color and temperature. In response to environmental conditions, they change their body color rather quickly, although it may take one or two molts before changes occur.

The role of this neuropeptide in the control of body color was examined by injecting the synthetic peptide into albino locusts (Tanaka, 2000a). Albino nymphs were variously treated during the 3rd instar and their body color was observed after ecdysis to the following instar. The results indicated that albino nymphs injected with the peptide at the beginning of the 3rd instar turned black completely after the following ecdysis. However, when a low dosage was applied, they developed purple, brown and dark brown colors. Nymphs injected at the end of the 3rd instar turned reddish without black spots in the 4th instar. These body colors were similar to solitary forms often encountered in the field. It should be noted that all albino nymphs were kept under crowded conditions. This suggests that albino nymphs can develop solitary body colors without experiencing low density or isolation if they receive appropriate dosages of corazonin at appropriate stages. Nymphs with gregarious body coloration also appeared when injected shortly after the mid stage of the 3rd instar.

Implantation of extra CA, a JH analog

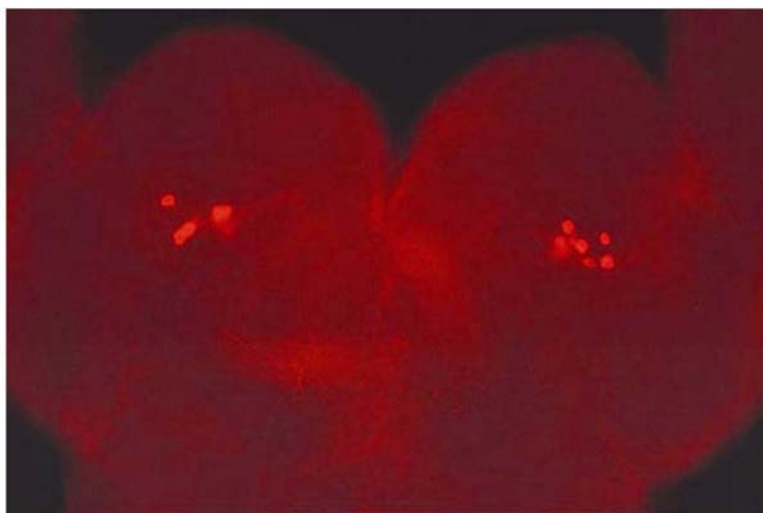


Fig. 3. Corazonin immunoreactivity (whitish spots) in the brain of *L. migratoria* (Photographed by L. Roller).

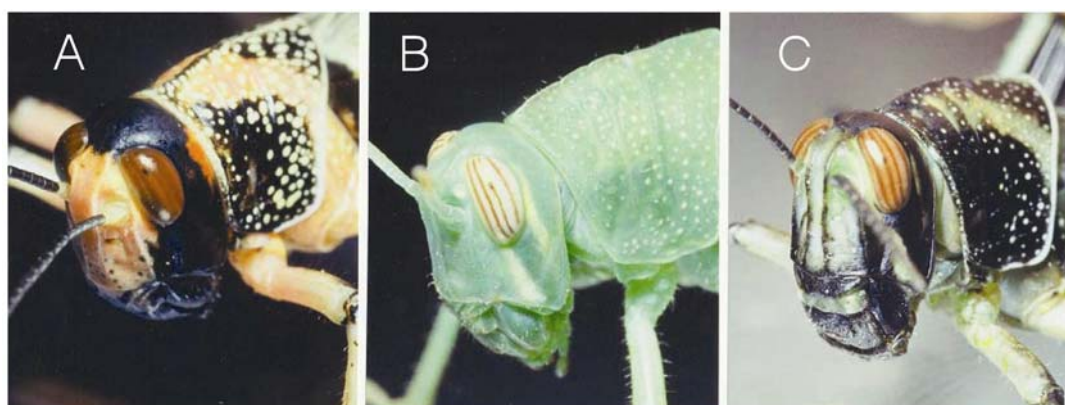


Fig. 4. Photographs showing crowd-reared (A) and isolated-reared (B and C) 4th stadium nymphs of *S. gregaria*. The nymph on the right (C) was implanted with 3 pairs of corpora cardiaca at the previous stadium. Note the black patterns on the body surface and the brownish pigment in the compound eyes that appeared after implantation (Reproduced from Tanaka and Yagi (1997) with permission of Entomological Society of Japan).

(methoprene) and JH III all induces green body color in albino nymphs (Tanaka, 1993; Hasegawa and Tanaka, 1994; Tanaka, 2000b). However, these nymphs fail to develop a brown or reddish color on the ventral surface and legs that is characteristically manifested by normal solitary green forms of this locust. Such body coloration can be obtained in albino nymphs only when both JH and

corazonin are injected (Tanaka, 2000b). Thus, green solitary nymphs require both JH and corazonin to express the characteristic body color. This neuropeptide is present in the CC and brain of both phases of a normal strain (Tanaka and Pener, 1994a).

These results appear to suggest that corazonin and JH may explain the body color polyphenism in *L. migratoria*. If

this is the case, one may expect that injection of corazonin would cause normal solitary nymphs to turn gregarious coloration without exposing them to crowding, and normal gregarious nymphs to turn even darker. It was demonstrated that such changes in body color actually could occur (Tanaka, 2000a, 2000b).

Body color polyphenism appears to be simpler in *S. gregaria* than in *L. migratoria*. In the former, solitary nymphs have a green or beige background color, whereas gregarious nymphs develop black patterns with an orange or yellow background color. As in *L. migratoria*, JH is responsible for the induction of the green color in this locust (Roussel and Perron, 1974; Mordue, 1977). Implantation of extra CC induced black patterns in green solitary nymphs (Tanaka and Yagi, 1997). In this case, the background green color was retained, but the compound eyes were strongly pigmented just like those of gregarious nymphs (Fig. 4; Tanaka and Yagi, 1997). We examined the role of corazonin in this locust by injecting the peptide into green solitary nymphs. Third instar nymphs injected with the peptide changed the body color after the following ecdysis and they became indistinguishable from gregarious ones of the same instar, in spite of the fact that they were kept in isolation continuously (Tawfik *et al.*, 1999). However, penultimate instar nymphs injected with the peptide developed black patterns after ecdysis to the last instar but failed to develop the reddish or yellow background color characteristic of that instar (Tanaka, 2001). Therefore, corazonin induces black patterns in late instars, and another factor is involved in the control of the background color in this locust (Tanaka, 2001), the situation being similar to that for *S. americana* in which the expression of the red wine background color is not influenced by injection of this peptide (Tanaka, 2004b).

The role of corazonin in the control of other phase-related characters

We tested the possible involvement of corazonin in the control of other phase-related characters by injecting the peptide into solitary locusts. The shape of pronotum is more convex in solitary (isolated-reared) individuals than in gregarious (crowd-reared) ones. In *L. migratoria*, injections of corazonin at the 2nd and 3rd instars caused solitary nymphs to develop a less convex pronotum in the last (5th) nymphal instar and the adult stage compared with that for oil-injected controls (Tanaka *et al.*, 2002a). In this case, it is important to separate individuals with different nymphal instars, because individuals with an extra (6th) instar tend to have more solitary characteristics than those with 5 nymphal instars. It was also demonstrated that injections of corazonin into solitary nymphs caused a shift in morphometric ratios of F/C and E/F towards the values typical for gregarious forms in *L. migratoria* (Fig. 5; Tanaka *et al.*, 2002a) and *S. gregaria* (Hoste *et al.*, 2002; Breuer *et al.*, 2003). In the latter, a significant effect was observed only in males. However, a subsequent study by Maeno *et al.* (2004) demonstrated that injections of corazonin into solitary (isolated-reared) nymphs caused a significant shift in F/C and E/F ratios in both sexes, as in *L. migratoria* (Tanaka *et al.*, 2002a). Furthermore, it was demonstrated that the earlier the injection during the nymphal stage the larger the 'gregarizing' effects of the peptide on these morphometric ratios in this species as well as *L. migratoria* (Maeno *et al.*, 2004).

The abundance of antennal sensilla is another conspicuous phase-related variation in locusts. Gregarious locusts have fewer olfactory sensilla on the antennae than solitary ones in *L. migratoria* (Greenwood and Chapman,

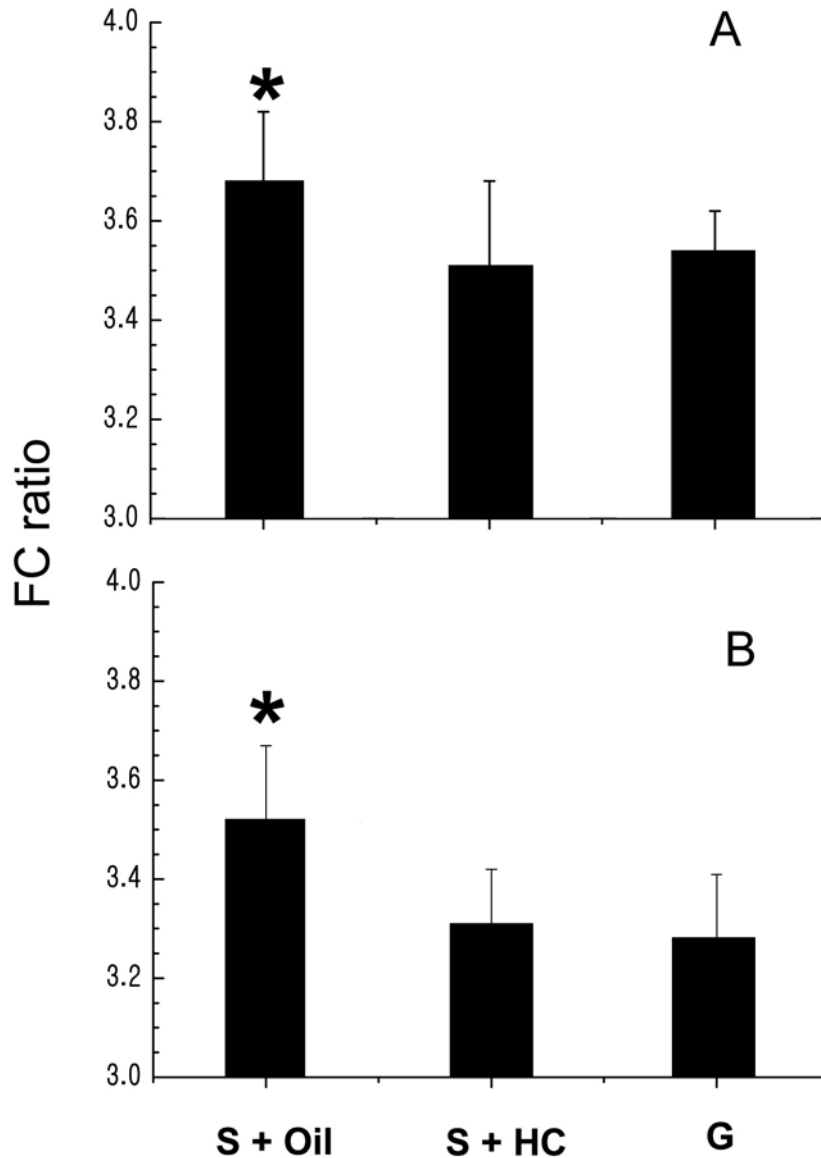


Fig. 5. The effect of corazonin injection on FC (femur length / head width) ratio in solitary (S, isolated-reared) adults in an albino (A) and a normal (B) strain of *L. migratoria*. The injections of oil (S+Oil, control) or corazonin (S+HC) were made at the 2nd and 3rd nymphal stadia. A group of locusts was reared under gregarious conditions (G). The asterisks indicate a significant difference by Mann-Whitney *u*-test (Based on Tanaka et al., 2002a).

1984; Heifetz *et al.*, 1994) and *S. gregaria* (Ochieng *et al.*, 1998). Because pheromones are important factors controlling locust behavior as mentioned above, antennal

sensilla, particularly olfactory receptors, should be important organs in the control of phase polyphenism. We thus tested the hypothesis that injection of corazonin

would mimic a crowding effect on the antennal sensilla in the two locusts. Solitarious locusts (reared in isolation) were injected with the peptide and the numbers of sensilla on certain antennal segments in the adult stage were compared with those for oil-injected controls or untreated gregarious locusts (reared in group). The results clearly indicated that the numbers of sensilla on those antennal segments were all reduced after injection of corazonin compared with those for oil-injected controls, but similar to those for gregarious individuals in *S. gregaria* (Maeno and Tanaka, 2004). A similar result was also obtained for *L. migratoria* (Yamamoto-Kihara, *et al.*, 2004).

Concluding remarks

The discovery of the Okinawa albino strain led us to identify the dark-color inducing factor in normal strains of *L. migratoria* and *S. gregaria*. As mentioned, Scham-corazonin was first isolated from *S. americana* without known function by Veenstra (1991). This grasshopper exhibits so-called green-brown polyphenism and variation in intensity of black patterns in response to environmental factors, particularly temperature (Tanaka, 2004a). Recently, Scham-corazonin was demonstrated to induce black patterns in this grasshopper by injection of this peptide (Tanaka, 2004b). However, it is getting clear that this neuropeptide influences not only body color but also body shapes and sensillum abundance on the antennae in locusts. The available evidence strongly suggests that this neuropeptide is important in the control of phase-related characters in locusts.

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飛蝗發育多型性之荷爾蒙調控

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摘 要

將近一世紀前，Uvarov(1921)提出發育多型性理論之後，陸續累積許多有關飛蝗的發育型改變及大發生的機制資訊。雖然經過許多早期學者的戮力研究，但是在荷爾蒙控制的體色及型態變化方面，仍不甚清楚。直到最近利用 *Locusta migratoria* 白化品系建立的生物檢定系統，從 *L. migratoria* 及 *Schistocerca gregaria* 身上萃取出，引起黑體色的神經胜肽和 corazonin 是相同的。注射 corazonin，不但可以引起不同獨居型若蟲體色變化，也能表現出群聚型若蟲體色特有的黑色和橙色(不管飼育的若蟲密度)。並且在獨居型若蟲注射 corazonin，會引起型態特徵的改變(體型及觸角的感覺器)與這二種飛蝗的群聚型成蟲相似。這些結果建議 corazonin 可能在飛蝗發育型相關之特徵調控上，扮演重要角色。

關鍵詞：黑化誘導激素、青春激素、發育多型性、飛蝗。