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Ecdysial growth of the filiform hairs and sensitivity of the cercal sensory system of the cricket, *Gryllus bimaculatus**

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Summary. 1. The ecdysial growth of cercal filiform hairs was investigated in the cricket *Gryllus bimaculatus*. The length of hairs varied from 40 to 500 μm in the 1st, from 40 to 650 μm in the 3rd and from 30 to 800 μm in the 5th instar nymphs (Fig. 1). Hemimetabolous development causes both hair growth and the appearance of new hairs at each ecdysis (Figs. 2, 3). The newly acquired hairs were shorter than 200 μm in every case (Fig. 4).

2. Velocity thresholds of cercal sensory interneurons (CSIs) to sinusoidal air-currents were measured in 3rd instar nymphs (Fig. 5A, B, C). CSIs 8-1 (medial giant interneuron: MGI) and 9-1 (lateral giant interneuron: LGI) showed threshold curves of acceleration sensitivity similar to those in adults. The thresholds for CSIs 8-1 and 9-1 were on the average higher in nymphs than in adults. The threshold curves for the two velocity-sensitive CSIs 10-2 and 10-3 were similar for nymphs and adults.

3. Velocity thresholds of cercal filiform sensilla were measured in 3rd instar nymphs (Fig. 6). In spite of the small size of nymphal hairs, the most sensitive ones showed the same sensitivity as did the long 1000 μm hairs of the adult.

4. The filiform hairs in 3rd instar nymphs were supported by a weaker spring than in adults (Fig. 7). Relative stiffness was about 50% of that in the long hairs in adults, but not much different than that in the short hairs.

5. Based on a theoretical estimation of hair motion, the threshold angle of a filiform sensillum in the 3rd instar nymph was calculated (Fig. 9). Threshold angles of the long sensilla seemed to be unchanged throughout hemimetabolous development.

Abbreviations: *CSI* cercal sensory interneuron; *LGI* lateral giant interneuron; *MGI* medial giant interneuron

* This paper is dedicated to the memory of the late professor Hiroshi Ikeda, Biological Institute, Faculty of General Education, Ehime University, Matsuyama, Japan

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Introduction

Hemimetabolous insects shed the exoskeleton (ecdysis) during post-embryonic development. The ecdysial change of cuticular structure occurs at all mechanoreceptor hairs: the hairs are shed, and new hairs take their place.

Size is an essential physical quantity of hair mechanoreceptors, because both the moment of inertia and the total deflecting torque applied from the medium vary with size (Shimozawa and Kanou 1984b). It is therefore possible that ecdysial growth leads to sensitivity changes of mechanoreceptor hairs. A change in sensitivity could cause a behavioral change to the same mechanical stimulus. We examined ecdysial change in the cercal sensory system of a cricket. We have measured the growth of hair structure and, somewhat paradoxically, have revealed that the sensitivity of the afferents remains constant.

Crickets and cockroaches have a large number of air-motion-sensitive filiform hairs on the cerci (Edwards and Palka 1974; Nicklaus 1965). Sensory stimuli to the hairs cause rapid escape behavior of the animals (Camhi and Tom 1978; Camhi et al. 1978; Bentley 1975). This is also true in the case of nymphal insects (Bentley 1975; Dagan and Volman 1982). In every case, cercal sensory interneurons (CSIs) carry the information along the ventral nerve cord (Kanou and Shimozawa 1984; Murphey et al. 1977; Tobias and Murphey 1979; Levine and Murphey 1980; Westin et al. 1977). In

crickets, the sense of atmospheric fluctuation is utilized not only for escape from predators, but also for defense against predators (Gnatzy and Heusslein 1986) and for recognition of nearby stridulating males (Kämper and Dambach 1979, 1981). Air motion is thus an important information bearing medium for these insects.

In adult crickets, the size of filiform hairs varies from 20 to 1500 μm in length and from 1 to 9 μm in diameter (Shimozawa and Kanou 1984b). Receptor sensitivity depends on hair size. Sensory afferents from long hairs respond to air velocity with low thresholds. The sensory afferents from short hairs respond to air acceleration with relatively high thresholds (Shimozawa and Kanou 1984a). The CSIs are also specialized to encode certain physical characteristics of air motion, either velocity or acceleration (Kanou and Shimozawa 1984). This is the result of length-specific convergence of sensory afferents onto each CSI (Shimozawa and Kanou 1984a). The acceleration-sensitive CSIs ultimately lead to the excitation of leg motoneurons whereas the velocity sensitive CSIs elicit inhibition of the motoneurons (Kanou and Shimozawa 1985). Any change in sensory properties due to the ecdysial growth of filiform hairs would affect the signal flow described above.

In this paper, we quantify the changes in mechanical properties of a hair sensillum at ecdysis. We also show the constancy of sensitivity in the cricket cercal system throughout post-embryonic development in spite of the ecdysial growth of the filiform hairs. The constancy of sensitivity is based in part on a coordinated growth pattern of cuticular structures, hair and spring, all of which have a common cell lineage (Lawrence 1966; Gnatzy and Romer 1980).

Material and methods

Animals. Nymphs of the cricket *Gryllus bimaculatus* were used. Animals reared in the laboratory were kept at a temperature of 28–30 °C (for details see Kanou and Shimozawa 1984).

Measurement of hair size. The length and diameter of cercal filiform hairs were examined with a scanning electron microscope (JEOL T-200). The cerci were isolated, air-dried and mounted on specimen stages, and sputter coated with gold before observation. The wholemount procedure permitted accurate measurement only of the hairs perpendicular to microscope axis. In order to measure numerous hairs in each specimen, hairs had to be aligned in one plane. Therefore, cerci were isolated in acetone and immediately flattened between two glass slides. The slides were removed after air-drying for 1–2 days.

The ecdysial change of filiform hairs (Figs. 3, 4) was examined by comparing one cercus of a newly molted nymph with its own exuviae (Fig. 2). Each hair was identified by its position relative to the other filiform, clavate and appressed hairs.

Measurement of thresholds of CSIs and of sensory afferents. We measured the velocity thresholds of CSIs and of cercal sensory afferents in 3rd instar nymphs and compared with those in adults previously measured (Shimozawa and Kanou 1984a).

Intact 3rd instar nymphs were pinned onto a cork board with ventral side up. A piece of sternum was removed carefully to expose the ventral nerve cord or the cercal nerve. The CSIs were penetrated with glass microelectrodes in the nerve cord between the 3rd and 4th abdominal ganglia. The CSIs were morphologically identified by intracellular marking with Lucifer Yellow CH. The marking dye was ionophoretically injected after making threshold measurements. Sensory afferents were penetrated at the cercal nerve with glass microelectrodes filled with 3 mol/l KCl.

The stimulus was a sinusoidal air-current generated by a pair of push-pull loudspeakers set at either end of an acrylic tube. Details of the stimulus equipment and threshold measurements have been described previously (Kanou and Shimozawa 1984; Shimozawa and Kanou 1984a).

Measurement of spring stiffness of the hair supporting apparatus. The stiffness of the spring which supports the filiform hair was measured by applying a small external force to the hair shaft. A small sphere of poly-methylmethacrylate was used to provide a known amount of gravity force (Shimozawa and Kanou 1984b). Spring stiffness is given by the ratio of hair deflection to the total torque due to the gravity force of the weight.

In all experiments, only L-hairs, which preferentially deflect parallel to the longitudinal axis of a cercus (Edwards and Palka 1974), were used. Spring stiffness was measured from hair shaft deflections in the preferential plane.

Estimation of angular deflection of filiform hairs. In order to estimate the deflection amplitudes of nymphal hairs to sinusoidal air-current stimuli, the numerical solution of the equation of motion of the filiform hair was computed by the Runge-Kutta method. The motion of the filiform hair is described as a second-order differential equation (Shimozawa and Kanou 1984b). The equation contains the coefficients of stiffness of the hair supporting spring and the moment of inertia of the hair. The moment of inertia was calculated from the hair size. The torque which deflects the hair is due to the drag force from the air-current. The drag-force is given theoretically by Oseen's method of Stokes's approximation of viscous force for a cylinder. The slender conical shape of the hair was approximated by a series of cylindrical segments. The boundary layer and velocity gradient of the air-current at the body surface were also taken into account.

We also determined the angular displacements of nymphal hairs from air-current stimuli at threshold by the same method used for adult hairs (Shimozawa and Kanou 1984b).

Results

Hemimetabolous growth of cercal filiform hairs

Both the size variation and the number of cercal filiform hairs increased in the course of post-embryonic development.

Figure 1 shows examples of size distributions of cricket filiform hairs for three nymphal stages (Fig. 1A, B, C). Hair length varied from 40 to 500 μm, from 40 to 650 μm, and from 30 to 800 μm in 1st, 3rd and 5th instar nymphs, respectively. The

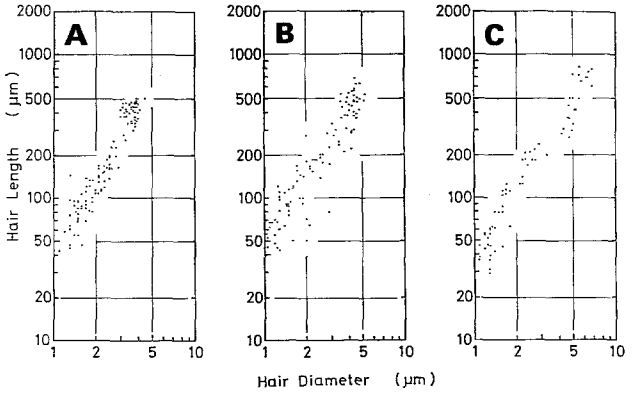

Fig. 1. Size distribution of cercal filiform hairs in the 1st (**A**), 3rd (**B**) and 5th (**C**) instar nymphs. Note scales are logarithmic. $n=120$ from 8 animals in the 1st, $n=58$ from 2 animals in the 3rd and $n=66$ from one animal in the 5th instar

hair diameter also varied from 1.1 to 4.5 μm, from 1.05 to 5.5 μm, and from 1.05 to 8 μm, respectively. Shorter and thinner hairs as well as longer and thicker hairs appeared in the later stages of development. Thus, the variation of hair size increased with development.

A comparison of nymphal cerci with their own exuviae revealed the morphological changes of individual hairs prior to and following ecdysis (Fig. 2). Among 385 hairs investigated before and after the first 3 molts, 2 hairs (0.5%) reduced their length by about 20 μm, 6 hairs (1.6%) did not change their length, and 377 hairs (97.9%) showed increases in length of about 4–340 μm following each ecdysis (Fig. 3). Longer hairs exhibited larger increases in length.

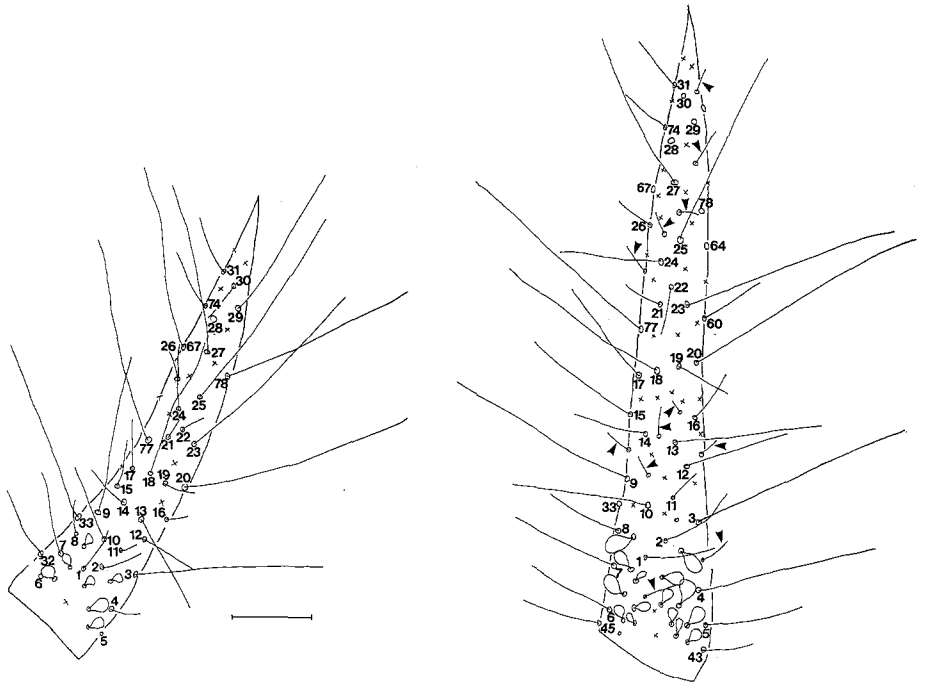

Fig. 2. An example of ecdysial changes of filiform hairs. One cercus of a newly moulted 3rd instar nymph (right) is compared with its own exuviae (left). Each hair was identifiable by the relative position to other filiform, clavate and appressed hairs. Numbers: identification codes of filiform hairs. Crosses: appressed hairs. Arrowheads: new hairs. Scale bar: 200 μm

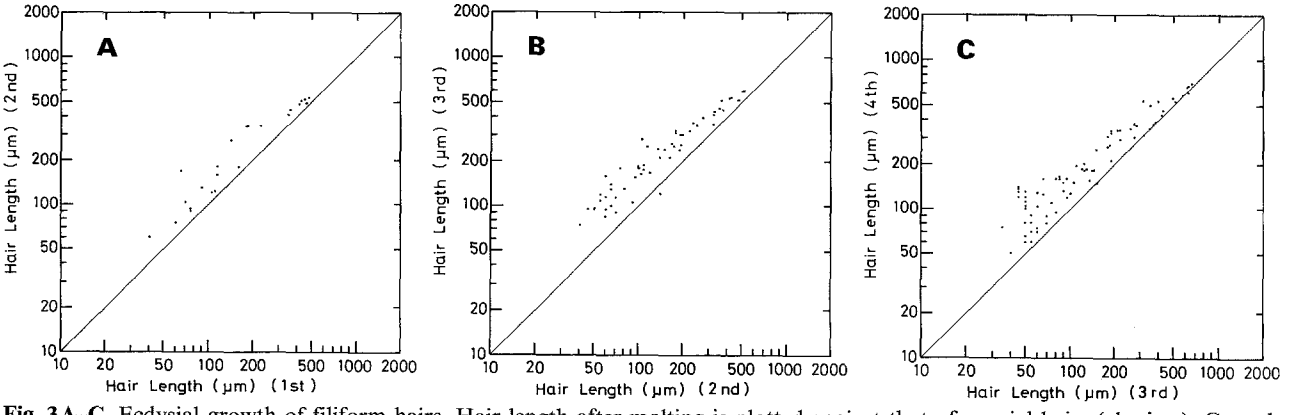

Fig. 3A–C. Ecdysial growth of filiform hairs. Hair length after molting is plotted against that of exuvial hairs (abscissa). Growth in the 1st (**A**), 2nd (**B**) and 3rd moltings (**C**). Data from one animal for each molting

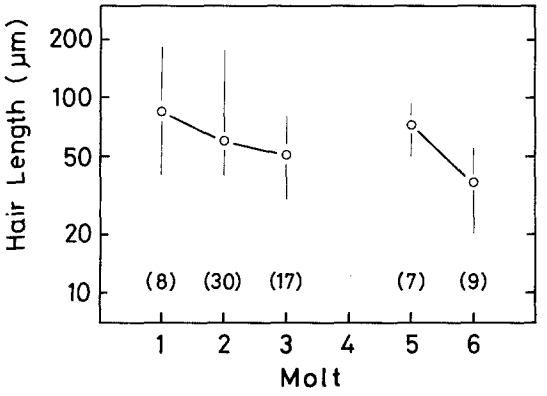

Fig. 4. Lengths of new hairs following ecdysis. Vertical bars: variations. Numbers in parenthesis: sample size

In addition to the growth of the hairs, new hairs appeared following each ecdysis (Fig. 2, arrowheads). The new hairs emerged evenly from the cercal surface, i.e. there were no specific regions to which the production of new hairs was restricted. The length of the new hairs was less than 200 μm after all molts (Fig. 4). Shorter hairs appeared at later stages.

Velocity thresholds of CSIs in 3rd instar nymphs

Thresholds of CSIs to a sinusoidal air-current stimulus were measured in 3rd instar nymphs. Due to their small size, we were unable to measure the velocity thresholds of CSIs in either 1st or 2nd instar nymphs. The threshold curves of CSI 9-1 from 3rd instar nymphs were similar to or higher than those of adults (Fig. 5A). This is also true in CSI 8-1 with one exception (Fig. 5B). The threshold curves obtained from CSI 8-1 varied more widely than in CSI 9-1. The sensitivities of CSIs 10-2 and 10-3 of 3rd instar nymphs were similar to those of adults (Fig. 5C). Because of short penetration times, the intracellular staining of CSIs 10-2 and 10-3 was sufficient only to mark the soma position. Therefore these two CSIs could not be distinguished from each other. As these CSIs have very similar thresholds in adults (Kanou and Shimozawa 1984), the threshold curves of the CSIs obtained from 3rd instar nymphs were lumped together.

Threshold of filiform sensilla in 3rd instar nymphs

Velocity thresholds of cercal filiform sensilla were also measured in 3rd instar nymphs (Fig. 6). The threshold curves of sensory afferents appeared to form two separate groups. Some of the sensory afferents showed relatively high, sloping threshold

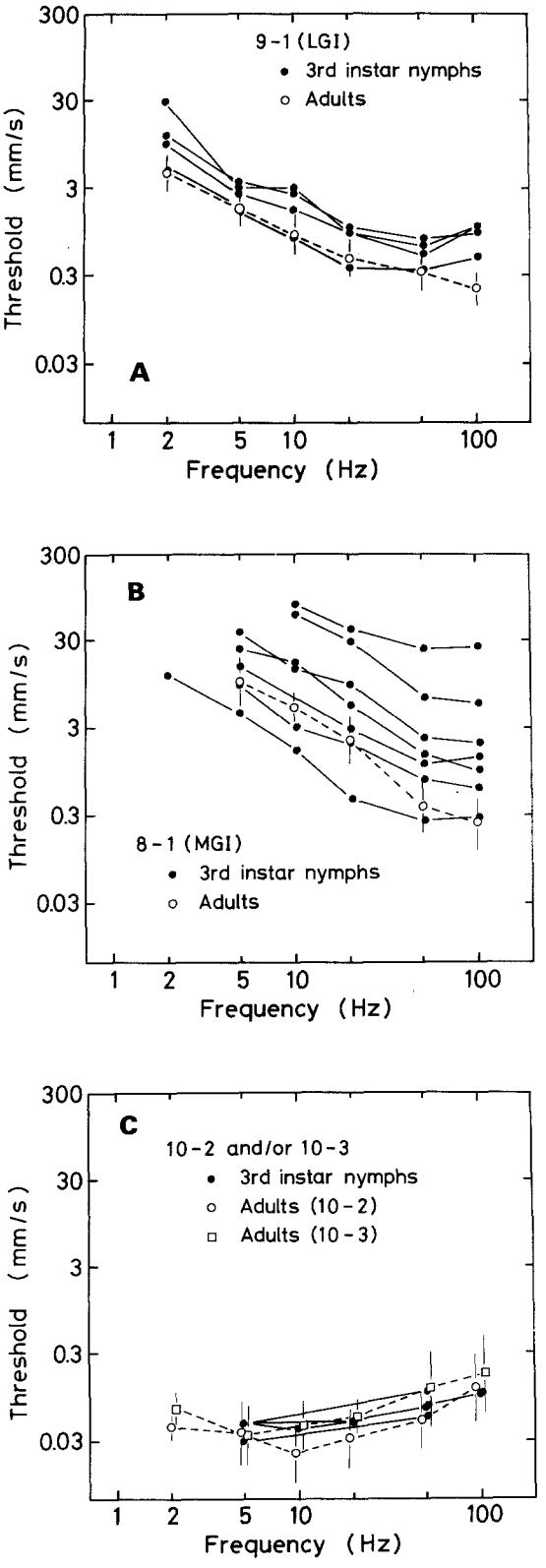

Fig. 5. Velocity thresholds of CSIs 9-1 (**A**), 8-1 (**B**) and 10-2 or 10-3 (**C**). Ordinate: peak velocity of sinusoidal air-current. Abscissa: alternating frequencies of stimulus air-current. Solid lines and filled circles: the 3rd instar nymphs. Dashed lines and open symbols: adults (from Kanou and Shimozawa 1984)

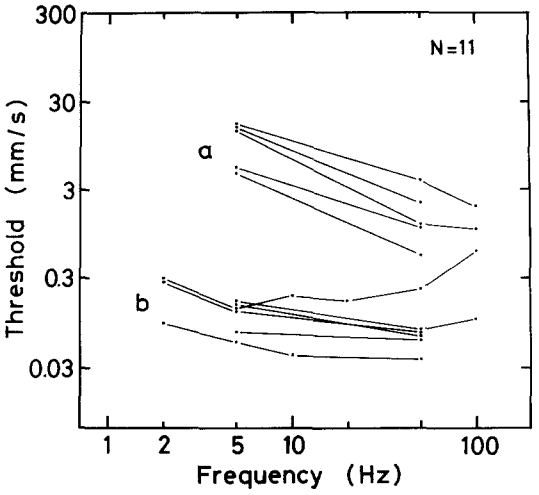

Fig. 6. Velocity thresholds of sensory afferents in the 3rd instar nymphs. Abscissa and ordinate as in Fig. 5. Thresholds of group *a* are similar to those of relatively short hairs in adults and group *b* are similar to long ones in adults (cf. Shimozawa and Kanou 1984a)

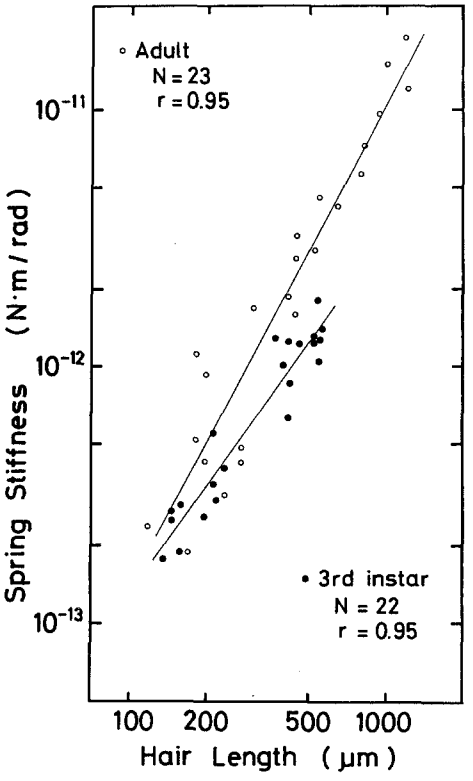

Fig. 7. Spring stiffness of hair supporting membrane. Open circles: adults. Filled circles: 3rd instar nymphs. Abscissa: hair length

curves (Fig. 6a). The other threshold curves were relatively low and flat (Fig. 6b). Due to the short penetration time, we were unable to measure the length of the filiform hairs of the recorded sensory afferents.

Although this apparent grouping might be an artifact of the small sample size, both types of threshold curves are characteristic of the adult sensory afferents as well (Shimozawa and Kanou 1984a). Threshold curves in group *a* resembled those of short, acceleration sensitive hairs in the adult. Threshold curves in group *b* resembled those of long, velocity sensitive hairs in the adults.

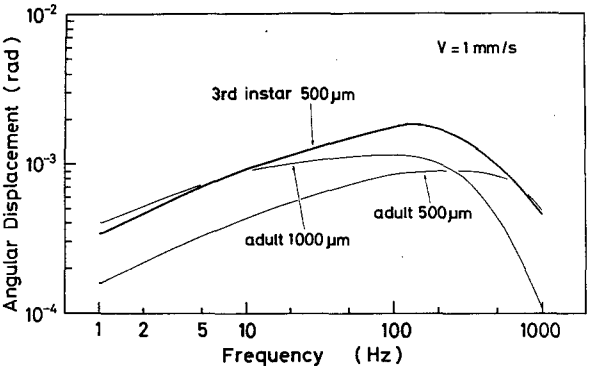

Fig. 8. Comparison of angular displacements of filiform hairs to sinusoidal air-currents (peak velocity: 1 mm/s). Theoretical estimation of deflections of a 500 μm hair in the 3rd instar nymph, a 500 μm hair in adult, and a 1000 μm hair in adult are drawn

Spring stiffness of the hair supporting apparatus and hair motion to air-current stimulation

The articulating membrane of filiform hairs in 3rd instar nymphs had less spring tension than that in the adult hairs (Fig. 7). The stiffness of the 500–600 μm hairs in the nymphs was about a half that of adult hairs of comparable length. Short 100–200 μm hairs showed little difference in the stiffness between adults and nymphs.

Based on the spring stiffness and the size of hairs in 3rd instar nymphs, we calculated theoretical estimates of deflection amplitudes to sinusoidal air-current stimuli. The deflection amplitudes calculated for the long (500 μm) hairs of 3rd instar nymphs were compared with those calculated for two adult hairs (Fig. 8). In 3rd instar nymphs, 500 μm hairs deflect twice as much as adult hairs of the same length. This difference in deflection results largely from the difference in spring stiffness. At low frequencies, long nymphal hairs show deflections similar to adult hairs approximately twice as long (1000 μm).

In the adult cricket, the long hairs are more sensitive than the short ones (Shimozawa and Kanou 1984a). Assuming that this is also true in nymphs, we theoretically determined the threshold angle of the long hair sensilla (Fig. 9). Most of the long hairs in 3rd instar nymphs were around 500 μm (Figs. 1B and 7). The threshold angle was

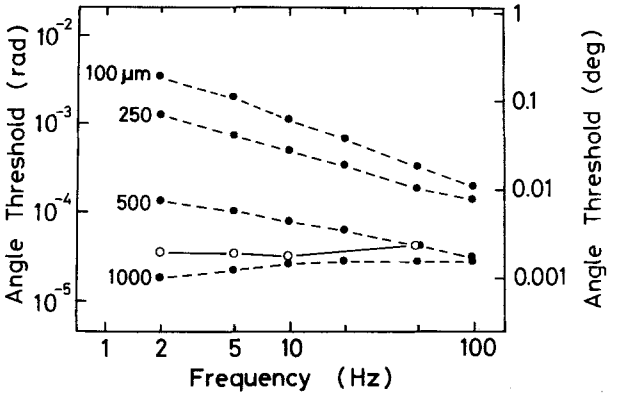

Fig. 9. Angle thresholds of filiform sensilla. Open circles and solid lines are of the most sensitive filiform afferents in the 3rd instar nymph (Fig. 6) estimated on the assumption that the hair is relatively long, i.e. 500 µm. Filled circles and dashed lines are the threshold angles in adult hairs at the lengths indicated (Shimozawa and Kanou 1984b)

estimated from the lowest sensory threshold curve (Fig. 6) and the calculated angular deflection of the 500 µm hair at threshold. From these theoretical estimates, the threshold angle of the nymphal 500 µm hair was similar to that of a 1000 µm adult hair (Fig. 9). The sensory cells associated with long hairs therefore have constant threshold angles throughout hemimetabolous development.

Discussion

At ecdysis, two changes occur in the cricket cercal sensory system: the existing filiform hairs enlarge and new, shorter hairs appear. The new short hairs become longer with each succeeding ecdysis. As a result, cricket cerci have more and longer filiform hairs at the later stages of development. Thus, crickets have a different sensory apparatus at each ecdysial stage.

This increase in the number of sensilla may improve the signal to noise ratio (S/N) of the sensory system. As the number of afferents converging upon an intereuron increases, the effect of any single sensory afferent is reduced, thus increasing the resolution of the graded response. The 1st instar nymph of the cockroach *Periplaneta americana* has only 2 filiform hairs on each cercus, and activation of a single hair evokes a turning escape response in all or none fashion (Dagan and Volman 1982). However, the activation of any single sensory cell of the 220 filiform hairs on the adult cercus evokes neither the turning behavior nor action potentials in any of the giant interneurons (Daley 1982).

The elimination of spontaneous discharge is also a type of S/N ratio improvement. An interneuron which responds only to a well synchronized volley from a greater number of sensory afferents filters out the spontaneity in the afferents without trading off absolute sensitivity. Alternatively, an interneuron could be a feature detector for a particular sensory stimulus if the threshold for spike generation is high and the inputs are appropriately weighted.

In contrast to the clear difference in number and size of hairs between nymphal and adult crickets, each CSI showed rather consistent types of threshold curves. CSIs 10-2 and 10-3 in 3rd instar nymphs showed the velocity sensitive threshold curves identical with those in adults. CSIs 8-1 and 9-1 in 3rd instar nymphs were acceleration sensitive as same as those in adults. Although the thresholds of CSIs 8-1 and 9-1 were slightly higher or more variable than in adults, the lowest threshold of each CSI in nymphs was close to that of the respective adult CSI.

Two sources could account for the variability of thresholds in nymphs. First, there might be a change in sensitivity of the mechanoreceptors during a single ecdysial phase. No attempt was made to determine the number of days until the next molting for any of the nymphs used. Nymphs at this stage molt at 3–4 days intervals. At the late phase of the inter-molt period, the filiform hairs are innervated by the tip of an elongated sensory dendrite passing through the ecdysial canal of the new hair. A new tubular body, the probable mechano-transduction site, forms underneath at the base of the new hair (Schmidt and Gnatzy 1971; Gnatzy and Romer 1980). Sensitivity also decreases during apolysis. In the caterpillar *Barathra*, which has eight vibration sensitive thoracal filiform hairs (Tautz 1977, 1978), animals become insensitive to an air-motion stimulus 1–2 hours before ecdysis (Gnatzy and Tautz 1977). Second, attenuation of the stimulus air-motion could be associated with the small size of the nymphs (6–7 mm in body length). Recording equipment such as the glass microelectrodes, the platform spoon and the cork board had to be set much closer to the cerci than in the case of adults. These two possible sources, however, can not explain the distinctive large variability in CSI 8-1.

Threshold curve measurements of single sensory afferents of filiform hairs were attempted in the 3rd instar nymphs. Although we could not determine the hair length because of the short recording time, the lowest threshold curve obtained was comparable both to those of 1000 µm adult hairs (Shimozawa and Kanou 1984a) and to adult CSIs 10-2 or 10-3 (Kanou and Shimozawa 1984). Given the same sensitivity, other properties in addition to

hair size must account for the difference between nymphal and adult sensilla. The hair-supporting springs were weaker in nymphs than those of equivalent hairs of the same length in the adults (Fig. 7). The angular displacement was the same in long hairs both in nymph and adult. Angle thresholds of sensory cells of long hair seemed to be unchanged as the sensilla develop from nymphs to adult.

The threshold curves of CSIs 10-2 and 10-3 in 3rd instar nymphs (Fig. 5C) can only be explained by the sensory input from the most sensitive afferents (Fig. 6). These CSIs in adults receive the sensory input from the afferents of the long, velocity sensitive hairs (Shimozawa and Kanou 1984a). The sensitivity of the most sensitive nymphal afferents is the same as those of the long hairs in adults. The long hairs in the nymph appear to grow into the long hairs of the adult. Therefore, it is most likely that the sensory afferents of the long hairs converge upon CSIs 10-2 and 10-3 in nymphs as well as in adults, though not proved exclusively.

We showed that the long filiform sensillum in the cricket cercal system maintains a particular sensitivity in spite of the ecdysial growth of its cuticular structure. Spring stiffness and hair length develop in close association with each other, while the threshold angle of the sensory cell seems unchanged. In hemimetabolous insects, the whole set of cells forming a sensillum – trichogen, tormogen, sensory and neurilemma – is differentiated from a single mother cell (Lawrence 1966). The trichogen cell and the tormogen cell secrete the hair shaft and the spring diaphragm, respectively (Gnatzy and Romer 1980). Coordination of ecdysial growth in the hair and of spring stiffness correlate with this common cell lineage. The derivation of a sensillum from a single mother cell during development may underlie the constancy of its sensitivity.

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