ANTENNAL GROOMING AND MOVEMENT BEHAVIOUR IN THE GERMAN COCKROACH, *BLATTELLA GERMANICA* (L.)

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Abstract—The antennal grooming behavior in *Blattella germanica* (L.), involves the coordinated use of the foreleg tibia and tarsus, and the mouthparts. The foreleg opposite the antenna is used to bend the flagellum to the mouthparts, after which it is pulled through the labium and maxillum by the resilience of the bend in the flagellum. Antennal grooming behavior is a sequence of five distinct events which define a grooming episode. Under normal conditions each antenna is groomed in 3–6 sec, and both antennae may or may not be groomed in successive episodes. When exposed to unfamiliar environments laboratory (VPI) and field (RHA) strain cockroaches display a distinct sequence of movement and antennal grooming rates (groomings/min) during the initial 5 min. Antennal grooming in both strains increases from the resting rate (0.23 = VPI, 0.95 = RHA) to the investigative rate (1.10 and 1.80 grooming per min, respectively) after 3 min exposure, but shortly returns to the resting rate. Response to a chemical and nonchemical stimulus rapidly increases the antennal grooming from the resting rate to the irritation rate, at which time the antennae collapse to the substrate.

INTRODUCTION

The primary function of grooming in cockroaches is cleaning various sensory organs. The parts of the cockroach body most often groomed possess important sensillae, including chemo- and mechanoreceptors on the legs (Frings and Frings, 1949; Brousse-Guary, 1981), and mechano-, hygro-, and thermoreceptors on the antennae (Roth and Willis, 1952; Ishii, 1971; Campbell, 1972; Ramaswamy and Gupta, 1981). As is the case in other insects, sensory organ systems in cockroaches are important for survival, and grooming may be an effective means of maintaining their responsiveness to the environment.

There is variation in the behavior patterns and the structures used for grooming in insects. Oral cleaning of the legs and antennae is common in the orthopteroid classes, and is thought to be the primitive condition for insects (Jander, 1966). Antennal grooming behavior in crickets, mantids, and cockroaches is similar; it requires coordinated movements of the head and foreleg to bend the antenna flagellum to the mouthparts (Zak, 1978a; Lefebvre, 1981; Metzger, 1995). Foreign material is removed from the flagellum after one or more passes through the mouthparts.

The general process of grooming the antennae has been described for *Blatta orientalis* L. (Hoffman, 1933) and *Periplaneta americana* (L.) (Ehrlich, 1943), but there have been few detailed studies of this behavior for the German cockroach, *Blattella germanica* (L.). Differences have been reported in the antennal grooming behavior of susceptible and insecticide resistant strains of this species when adults were exposed to insecticide vapors (Bret and Ross, 1986) and when exposed to surface residues (El-Awami and Dent, 1995; Zhai and Robinson, 1995). The objectives of the research presented here were to describe the structures and processes of antennal grooming behavior of the German cockroach, and to describe the influence of environmental conditions and walking movement on antennal grooming in a laboratory and field strain of this species.

MATERIALS AND METHODS

The hypothesis-free experimental design of this study is a function of the objective to describe the events of antennal grooming behavior, and the influence of environmental conditions on this behavior. A combination of repeated observation and experimentation procedures were employed using individual cockroaches in controlled environments.

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Insects

Adult male German cockroaches were taken from two strains: VPI, a susceptible strain reared in the laboratory for approximately 190 generations; and RHA, a pyrethroid and organophosphate resistant field strain (Zhai and Robinson, 1991; 1996) from urban apartments in Roanoke, VA, USA. Antennal grooming behavior was observed primarily on RHA. All observations were conducted under conditions of 55–65% RH and 22–24 C, during the day and night (1900–2100 h) under fluorescent light. The cockroaches were maintained under continuous light conditions to limit possible rhythmic activity (Dreisig and Nielsen, 1971).

Unstimulated Antennal Grooming Behavior

Cockroaches were observed individually on 9×9 cm glass plate covered with a clear plastic lid. The 8 mm height of the lid confined the cockroach to the surface of the plate without the use of petroleum. Individual cockroaches were provided 1 hr acclimation on a glass plate before permitted to walk onto another plate for observation. Grooming behavior of 20 individual cockroaches was observed and recorded for 20 min each. Additional observations were conducted by placing individual cockroaches in clean plastic petri dishes and observing antennal grooming behavior under magnification. Red-pigmented dust placed on the antennae of cockroaches was used to identify portions of legs, antennae and mouthparts involved in grooming.

Stimulated Antennal Grooming Behavior

Cockroaches were prepared as described above for the observation of antennal grooming, except that after acclimation they were permitted to walk onto plates containing 0.0308 g per sq cm of insecticide dust (deltamethrin, 0.05% [AI], AgrEvo, Montvale, NJ) or the same amount of an inert dust. The number of antennal groomings per min performed by 10 individual cockroaches was recorded for 15 min.

Exploratory Behavior and Grooming

Cockroaches were prepared as described above for the observation of grooming. After acclimation the cockroaches were permitted to walk onto a clean plate which was then covered with a clean plastic lid. The new plate and lid were considered to be a new environment. The number of antennal groomings per min performed by 20 individual cockroaches in this environment was recorded for 5 min.

Cockroach movement was examined to determine the movement rate (movement units per min) on insecticide-treated and untreated plates. Individual cockroaches were observed walking on plates in daylight conditions. The plastic cover used to confine the cockroach to the plate was marked into 9 squares (2.8×2.8 cm), and each square assigned a value of 1 movement unit. Each cockroach was confined on a clean plate for at least 20 min before it was moved onto a treated plate for observation. One movement unit was awarded to a cockroach when all six legs entered a different square during walking. The movement units were totaled each min for 5 min.

RESULTS AND DISCUSSION

Events of Antennal Grooming Behavior

Antennal grooming behavior consists of the following sequence of events: 1) medial rotation of the head coincides with the raising and extending of the foreleg opposite (contralateral) the antenna to be groomed; 2) the flagellum in the region of annuli 15–20 is contacted by the fore tibia and adduction of the foreleg bends the flagellum to the mouthparts; 3) the foreleg returns to the substrate; 4) rapid lateral movement of the maxilla and labium on the flagellum as it moves through the mouthparts; and 5) the flagellum returns to the original, extended position, and the maxilla and labium continue to move for a short time. This sequence of five events comprises one episode of antennal grooming.

An episode is defined as the complete grooming of one antenna, and does not involve any other grooming activity, including another antenna. Under normal condition, both antennae may not be groomed in successive episodes. The activity of the cockroach following an antennal grooming episode is unpredictable; it may include grooming the maxillary palps, forelegs, antenna, or it may resume walking or remain still.

Events 1 and 2 (Fig. 1). The initial events of antennal grooming are completed in a continuous motion. Grooming begins with the slightly downward and medial rotation of the head in the direction of the extended foreleg; this movement facilitates the contact between the fore tarsus and the opposite antenna. The region of the 15–20th annuli of the antenna is contacted by the basal third of the foretarsus. After contact with the flagellum the leg moves in a posterolateral direction which guides the flagellum to the mouthparts. This is followed by slight retraction of the maxillary and labial palps to a position close to the flagellum. The palps remain bent and the apical segments may contact the flagellum.

After grooming of an antenna marked with pigmented dust, small amounts appear on the base of the tarsus and on the apical segment of the maxillary palps. The presence and location of the pigmented dust indicates the contact points with the flagellum during grooming. Zak (1978b) reported similar movement of the head, foreleg, and flagellum at the onset of antennal grooming in a mantis. He concluded that this coordinated movement may be linked to interactions between segmental motor centers, located in the subesophageal ganglion, which control the mouthparts and some neck muscles, and the prothoracic ganglion, which also controls neck and foreleg muscles (Zak, 1978b). The procedure of contacting the antenna with the opposite foreleg and bending the flagellum to the mouthparts is common among cockroaches (Hoffman, 1933; Ehrlich, 1943; Luco and Aranda, 1964), but not for some related insects. For example, in a field cricket the flagellum is brought in contact with the mouthparts by the near foreleg (Lefebvre, 1981). In a mantis the opposite foreleg is used; however, the near foreleg may be substituted following amputation of the opposite foreleg (Zak, 1978b).

Antennal grooming in *B. germanica* usually does not involve the basal 15–20 segments of the 80–92 segments of the adult flagellum (Campbell, 1972). Few sensillae with chemo- and mechanoreceptive functions are located on these segments, but are more common on the middle segments (Ramaswamy and Gupta, 1981). These middle segments of the flagellum are usually included in the grooming process. The number of chemoreceptive sensillae increases from the base of the flagellum to the middle, and decreases thereafter. The 10 basal flagellar segments of adult female *B. germanica* lack thin-walled chemoreceptors, and males have thin-walled chemoreceptors beginning on segment 5 (Ramaswamy and Gupta, 1981). Although thick-walled chemo- and mechanoreceptors are found on all antennal segments, they are most numerous in the middle third of the flagellum. Hygroreceptive sensillae are located after segment 11 of the flagellum (Roth and

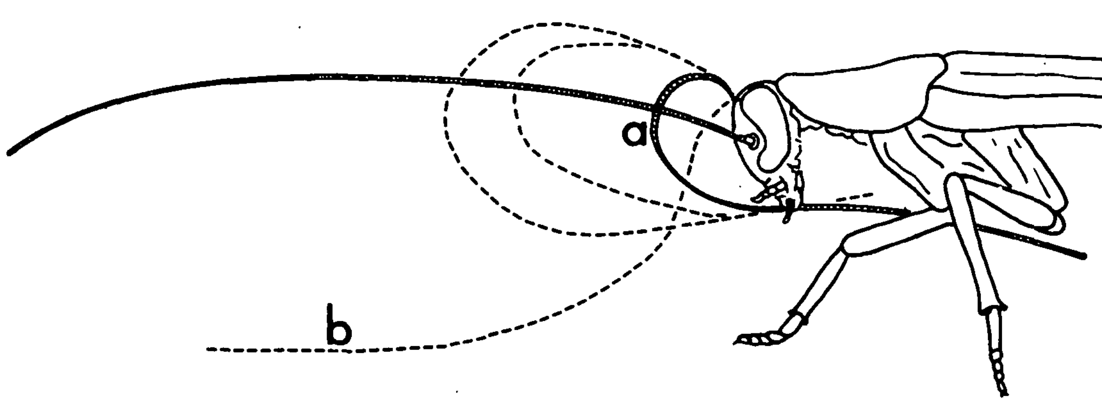

Figure 1. Antennal grooming in *Blattella germanica;* a, normal bend in the flagellum at the start of the mouthing part of grooming, dotted lines depict the gradual movement of the flagellum through the mouthparts; b, antenna collapsed to the substrate.

Willis, 1952). As a result of their apical location of these receptors would be cleaned during normal antennal grooming behavior.

Antennal grooming is a regular component of the resting and active state of *B. germanica*; however, the frequency of this behavior may differ among strains. Zhai and Robinson (1996) reported differences in the antennal grooming rate of VPI and RHA males on clean glass after 20 min acclimation: VPI groomed their antennae about once every 4 min ($\bar{x}$ 0.23 groomings per min), RHA groomed their antennae about once every minute ($\bar{x}$ 0.95 groomings per min). These rates are considered the resting rate for antennal grooming in VPI and RHA. Antennal grooming may also be performed in response to stimulation of sensory receptors on the antennae, or regions of the head and legs. Increased grooming by VPI and RHA in response to exposure to insecticide vapors and residues have been reported by Bret and Ross (1986) and Zhai and Robinson (1996).

Event 3. After bending the flagellum to the mouthparts, the foreleg returns to approximately the position and location on the substrate as before the start grooming. Occasionally, the foreleg may not completely return but remain for several seconds in a position that is about halfway between the substrate and the antenna. The foreleg returns to the substrate before the end of the grooming episode.

Event 4 (Fig. 2). This event is the mouthing part of the grooming, and is characterized by the continuous movement of the mouthparts around the flagellum as it moves through them. Mouthing begins immediately when the flagellum is brought to the mouthparts, and continues for several seconds after the flagellum exits and returns to the original position. Mouthing is the actual cleaning process of antennal grooming. During this process the maxillae move rapidly, and the maxillary palps are often bent with the apical segment close to the flagellum. The labium also moves, as do the labial palps.

The small medial groove of the labrum, and the opening between the glossa and paraglossa of the labium apparently function to center the flagellum at two points along its length as it passes through the mouthparts. The labral groove positions the anterior portion of the flagellum below the

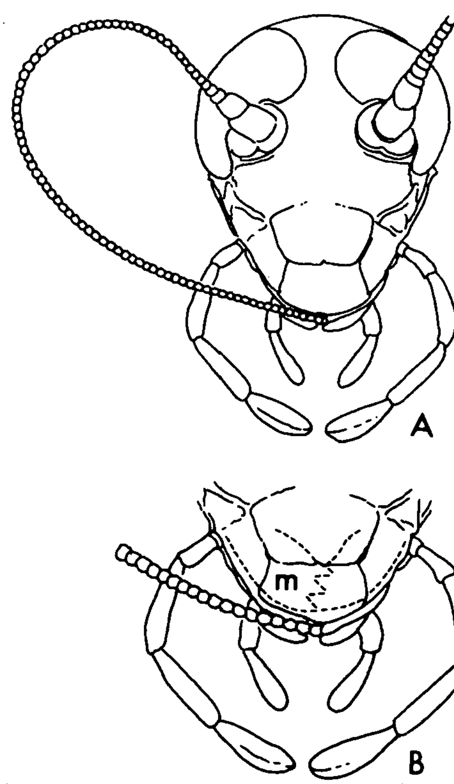

Figure 2. Anterior view of the head of *Blattella germanica*. A. Antenna flagellum in the mouthparts during the mouthing part of grooming. B. Anterior of the head showing flagellum in mouthparts and the position of the mandibles (dotted line) above the flagellum as it passes through the mouthparts.

level of the closed mandibles, which open and close rapidly during the mouthing portion of grooming (Fig. 2). Without the anterior labral groove and the opening between the posterior glossa and paraglossa of the labium providing two-point centering and retention of the flagellum below the level of the mandibles (Fig. 2B), the flagellum might be severed by the mandibles during the mouthing process.

The mouthparts do not function to move the flagellum anteriorly during grooming. Instead, they contain the flagellum and remain in continuous motion as the flagellum is "pulled" through the mouthparts at nearly a constant speed by the resilience of the bowed antenna. The blood-filled flagellum naturally resists bending, and returns to its original, extended position when it leaves the mouthparts. The limited amount of bending possible by the flagellar segments, and the pressure probably provided by the haemolymph appear to provide the resilience.

The cleaning aspect of antennal grooming is primarily a scraping action. As the flagellum moves between the mouthparts (mouthing), debris is removed and accumulates on the posterior surface of the glossa and paraglossa. Material on the cylinderical-shaped flagellum is scraped off as it passes between the paired glossa because the pliable integument of these structures surrounds the well-sclerotized and hardened flagellum. Debris is removed by the scraping action achieved by pulling the flagellum through the glossa. Except for what may drop to the substrate, debris that collects on the glossa and paraglossa is usually manipulated into the mouth and ingested when grooming is completed. This is confirmed by the appearance of red color in the esophagous following the grooming of antennae marked with pigmented dust.

Zak (1978a) reported that the duration of the mouthing portion of grooming in a mantis was influenced by feedback from receptors located in the mouthparts. In *B. germanica* the duration of the mouthing depends on the length of the flagellum; it lasts 3–6 sec for a flagellum of normal length. Campbell (1972) reported that the marginal sensilla located on the basal 20–24 segments of the adult German cockroach antenna may act as campaniform organs and respond to the bending of the flagellomeres. They may play a role in determining the duration of mouthing by limiting the degree of bending of the flagellum. Chemoreceptors at the base of the paraglossa (Frings and Frings, 1949) may influence the ingestion of some of the debris that is removed from the antennae during cleaning.

Event 5. When the apical segments of the flagellum move completely through the labrum the antenna returns to the extended position. However, the mouthing usually continues for several seconds after the flagellum is groomed. The period of continued mouthing is the final event of the grooming process.

The apical segments of the flagellum are usually groomed longer than preceeding segments. This may be the result of reduced resilience as the bend in the flagellum decreases and the speed slows as it moves through the mouthparts. Hoffman (1933) reported that at the conclusion of antennal grooming the end of the flagellum of *B. orientalis* may be retained in the mouthparts for several minutes, and during this time the terminal segment may be removed. Woodruff (1937) reported similar self amputation of the flagellum tip in *B. germanica*. However, close examination of antennal grooming behavior indicates that amputation may be the result of the tip of the flagellum slipping into the path of the moving mandibles and being accidently severed.

Movement and Antennal Grooming

VPI and RHA displayed distinct movement and grooming behavior during the 5 min exposure to the new or unfamiliar environment. During the 1st min the amount (movement units per min) of movement increased to the searching rate, then steadily declined until the 3rd min, at which point it stablilized close to the resting rate. The searching rate of movement was approximately 2-fold greater than the resting rate for both strains. The amount (grooming episodes per min) of antennal grooming increased during the first 1–2 min of exposure, and attained the investigative rate at about 3 min. The investigative rate for VPI and RHA was 2–5 fold greater than the resting rate. The investigative rate is sustained for only 1–2 min before grooming activity returned to the resting rate.

Resting and searching rate of movement. After 1 min exposure to a new environment VPI and RHA attained a movement rate of 28.5 (SD, 13.7) and 38.9 (SD, 13.1) movement units per min, respectively; this is considered the searching rate for these two strains (Figs. 3, 4). At 2 min of exposure the movement rates for VPI and RHA were 20.1 (SD, 9.9) and 30.5 (SD, 12.4), respectively; and after 3 min the movement rates decreased to 17.9 (SD, 6.9) and 25.2 (SD, 9.7) movement units per min, respectively. At 5 min exposure the movement rates decreased to the resting rate of 15.1 (SD, 6.1) and 18.7 (SD, 7.8) movement units per min, respectively.

Darchen (1952, 1955) concluded that there were certain novel elements (thresholds) in the environment that brought forth exploratory activity *in B. germanica*, and that the distance traveled during this activity steadily declined during a 15 min period. At the end of the movement phase of exploratory activity, Darchen (1955) reported that the antennae became involved in exploring the new environment, as indicated by increased antennal movement and grooming. Others have reported similar behavior patterns for laboratory and field strains of the German cockroach. For example, differences between VPI and RHA in foraging activity and exploratory behavior in a new environment were reported by Akers and Robinson (1983), and Zhai and Robinson (1992).

Resting and investigative rate of antennal grooming. After 1 min exposure to a new environment the amount of antennal grooming was nearly equal to the resting rate for VPI and RHA, which is 0.23 (SD, 0.01) and 0.95 (SD, 0.14) groomings per min, respectively (Zhai and Robinson, 1996) (Figs. 3, 4). At 2 min exposure the grooming rate for VPI and RHA was 1.0 (SD, 0.03) and 1.70 (SD, 0.02), respectively; after 3 min exposure the grooming peaked at 1.10 (SD, 0.48) and 1.81 (SD, 0.03) groomings per min, respectively. These peak rates are the investigative rate. After 5 min exposure the grooming rate decreased to 0.47 (SD, 0.24) and 0.56 (SD, 0.29) groomings per min for VPI and RHA, respectively.

Irritation rate of antennal grooming. Exposure to an environment containing an insecticidal or noninsecticidal dust increased the antennal grooming in RHA above the investigative rate to an irritation rate which is 1.4–2.5 fold higher than the investigative rate.

When RHA were exposed to plates containing 0.0308 g per sq cm of inert dust, antennal grooming increased from the resting rate of 0.95 groomings per min to a mean of 2.1 and 2.5 grooming per min at 8 and 10 min, respectively. At 12 min exposure to the dust antennal grooming reached a peak of 2.3 grooming per min; however, by 12 min a mean total of 28.5 (SD, 0.86) grooming episodes were performed, and the antennae collapsed to the substrate. The antennal-collapse response was similar following exposure to the deltamethrin dust residue of 0.0308 g per sq cm, but collapse occurred in approximately half the time (6 min). At 4 min exposure a mean total

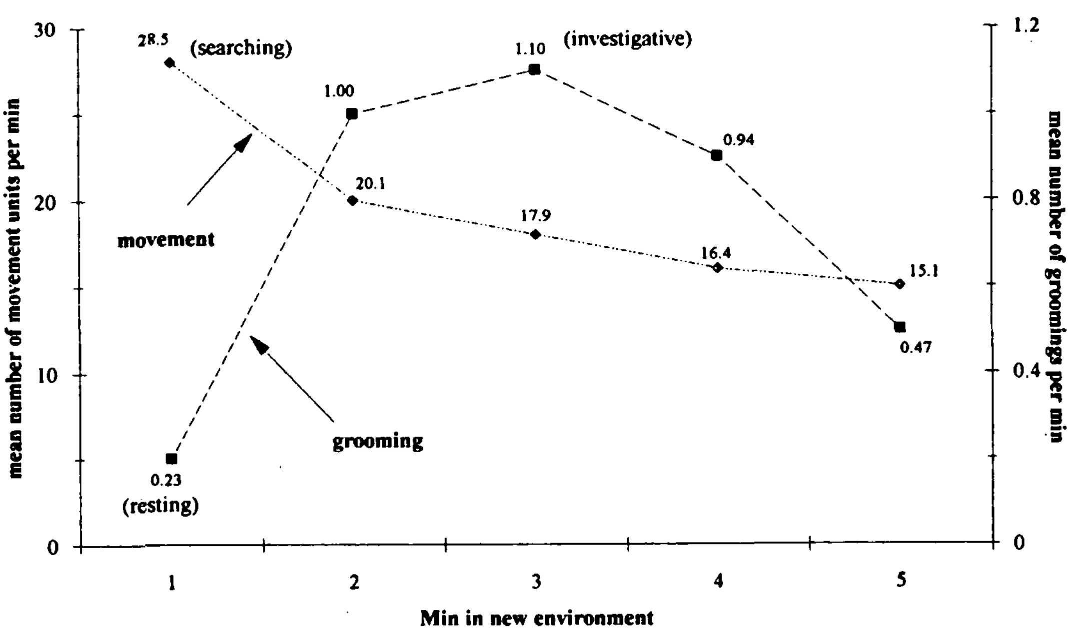

Figure 3. Mean number of movement units and antennal groomings per min during the first 5 min VPI strain German cockroaches are exposed to a new environment.

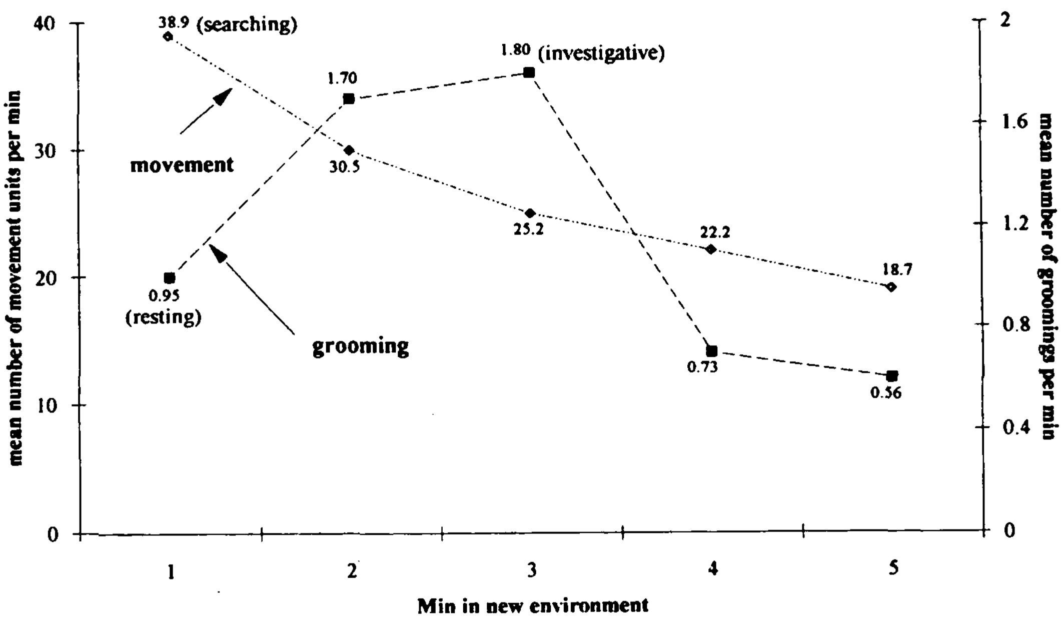

Figure 4. Mean number of movement units and antennal groomings per min during the first 5 min RHA strain German cockroaches are exposed to a new environment.

of 18.7 (SD, 0.61) grooming episodes were performed and the the grooming rate was 4.6 groomings per min, and by 6 min exposure a total of 27.6 (SD, 0.74) grooming episodes were performed and both antennae collapsed.

Antennal collapse. The irritation rate of antennal grooming was not sustained for more than 27–30 grooming episodes within approximately 12 min without collapse of the antennae. After this large number of groomings within such a short time period antennal turgor seems to diminish and they no longer remain erect; the collapsed antennae lie on the substrate in front or to the side of the cockroach. Although the collapse of the antennae is bilateral, it can result from the grooming of both or the exclusive grooming of only one antenna. While on the substrate the antennae usually continue to move, and antennal grooming behavior may continue. Grooming performed while the antennae are collapsed results in the flagellum being bent closer to the front of the head, and the segments close to the base are cleaned by the mouthparts (Fig. 1). The antennae return to their normal, erect position after 4–6 min on the substrate.

Without the resilience of the bowed antenna, the flagellum of a collapsed antenna is not effectively pulled through the mouthparts to complete the mouthing event of grooming. Grooming that is initiated while the antennae are collapsed often results in the flagellum remaining stationary in the mouthparts and during this time one portion may receive extended mouthing. The difficulty of grooming collapsed antennae provides additional evidence that it is the resilience in the bent and blood-filled flagellum that pulls it through the mouthparts.

CONCLUSIONS

Antennal grooming has an important role in the survival and success of *B. germanica* in the domiciliary environment. Periodic acts of antennal grooming probably improve sensory input and behavioral responsiveness to aspects of the environment, such as locating food, harborage, and sexual partners. Information about the substrate and the chemical environment may also be received by receptors on the antennae.

The searching and grooming behavior reported here is consistent with the exploratory behavior described by Darchen (1952, 1955, 1957), Darchen and Richard (1960), and Sommer (1978) for *B. germanica*; by Bell and Kramer (1979) and Turillazzi et al. (1980) for *P. americana*. Darchen (1955) considered exploratory behavior the strongest overall trait in the behavior repertoire of *B. germanica*, and antennal grooming and movement were two of the major components. Since these two components are mutually exclusive, i.e. the cockroach must momentarily cease walking to begin antennal grooming, their hierarchial organization and frequency can be used to characterize exploratory behavior. During this behavior the amount of movement increases from a resting rate to a searching rate, then returns to the resting rate, and antennal grooming increases from the resting rate to the investigative rate, then returns to the resting rate. As unpredictable as the occurrence of movement and grooming may be in response to normal conditions, this sequence appears predictable when the insect encounters an unfamiliar environment (Darchen 1952, 1955).

In the domiciliary environment the German cockroach spends a majority of time aggregated and nearly inactive in a harborage. Only a limited time is spent outside the harborage searching for food, water or a mate. The two phases of foraging activity reported for *B. germanica* are from 1400–1700 h and from 2200–2300 h (Dreisig and Nielsen, 1971; Sommer, 1975). Within a harborage the individual cockroaches are relatively inactive, and there may be need for only limited antennal or leg grooming. However, when a German cockroach leaves the harborage it is very likely to encounter unfamiliar conditions even if it moves a short distance. Cockroaches will actively investigate new environments (Darchen, 1955), and perhaps the most important activity for a cockroach in a new environment is to locate a harborage. The rapid searching along the perimeter of the immediate environment that is characteristic of *B. germanica* (Darchen, 1952; Sommer, 1978) may be associated with a search for a suitable harborage. It is likely that this behavior also facilitates recognition of topographic aspects of the environment, which may later provide an advantage for foraging or retreating to a harborage.

The second most important action for a cockroach in relation to survival in a new environment may be antennal grooming. This action may occur after searching has or has not found a suitable harborage, and it places the sensory organs on the flagella at peak responsiveness to provide the insect with a variety of information about the immediate environment. The presence of volatile organic compounds may indicate food or insecticides, and pheromones can provide information on the sex, abundance and perhaps location of conspecifics in the new environment.

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