Chapter 11
Functional Coupling of Cercal Filiform Hairs and Campaniform Sensilla in Crickets

Ralph Heußlein, Heribert Gras, and Werner Gnatzy

11.1 Introduction

The cerci, paired appendages at the rear end of the cricket abdomen, are covered with a variety of sense organs: the mechanosensitive filiform, clavate and long bristle hairs as well as campaniform sensilla and the gustatory short bristle hairs (Gnatzy and Schmidt, 1972, 1972; Schmidt and Gnatzy 1972). In this multimodal receptor system (Murphey and Chiba 1990), the most numerous are the exclusively mechanosensitive receptor types: filiform hairs and campaniform sensilla.

A characteristic feature of the cricket cerci in contrast, for example, to those of cockroaches (Gnatzy 1976) is that the larger filiform hairs are morphologically and functionally coupled with campaniform sensilla (Dumpert and Gnatzy 1977). The campaniform sensilla, positioned on both sides of the socket of long filiform hairs (Gnatzy and Schmidt 1971), are cuticular stretch receptors. They respond to deflection of the socket, which can occur when the cercus is touched (Gnatzy and Heußlein 1986) or as a result of strong air movement (Dumpert and Gnatzy 1977). The filiform hairs, about 800 per cercus, differ from one another in the length of the shaft (*Acheta domesticus*: ca. 30–1500 μm, Edwards and Palka 1974; *Gryllus bimaculatus*: ca. 100–3000 μm, Knyazev and Popov 1981), the preferred plane of oscillation and the direction of movement that causes the receptor cells to depolarize (Dumpert and Gnatzy 1977; Palka et al. 1977; Knyazev 1978; Tobias and Murphey 1979; Gnatzy and Tautz 1980; Knyazev and Popov 1981; Kanou et al. 1989).

Correlated with the number of campaniform sensilla located near the socket of filiform hairs (up to three in *Acheta*: Edwards and Palka 1974; up to five in *Gryllus*: Gnatzy and Schmidt 1971; Knyazev and Popov 1981), different filiform-hair size classes can be distinguished (see Knyazev and Popov 1981). The cercal filiform hairs themselves are highly sensitive detectors of air-particle movement. The forces exerted by the moving air particles deflect the hair shaft from its resting position.

W. Gnatzy (✉)
Institut für Ökologie, Evolution und Diversität, Goethe-Universität, Siesmayerstr. 70, 60323 Frankfurt am Main, Germany
e-mail: Gnatzy@zoology.uni-frankfurt.de

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The oscillatory behavior of the shaft, especially the frequency dependence of amplitude and phase, has been studied by Kämper and Kleindienst (1990) and Kumagai et al. (1998a).

The responses of the sensory cells, in particular their sensitivity and frequency response, are determined by both morphological parameters (see Gnatzy and Tautz 1980; Shimozawa and Kanou 1984a; Kanou et al. 1988; Kumagai et al. 1998b) and physical principles (Markl 1973, 1978; Fletcher 1978; Tautz 1979; Henson and Wilkens 1979; Shimozawa and Kanou 1984b; Kämper and Kleindienst 1990; Humphrey et al. 1993; Landolfa and Miller 1995; Shimozawa et al. 1998). However,

Fig. 11.1 Head-stand and defensive kick of an adult male *Acheta domesticus* in response to an attack and tactile stimulation by a hunting female of *Liris niger* (Sphecidae, Hymenoptera): Crickets can repulse animals that touch their body by kicking backward with the ipsilateral hindleg. Such a tactile stimulus, in natural situation e.g. by the antennae of a female *Liris niger* or under experimental conditions light touching by a small paint brush, leads to a tipping movement of the cuticular socket in which each cercal filiform hair is inserted. Ultimately this stimulates campaniform sensilla which are morphologically and functionally coupled with larger cercal filiform hairs (Dumpert and Gnatzy 1977). The stimulation of the campaniform sensilla then releases the kick-movement of the cricket's hindleg. There are no pauses between the different phases of the kicking process (pulling up the leg, the actual kick, and the return to the ground) so that the total movement is often completed within less than 100 ms (Hustert and Gnatzy 1995)

as those recent studies have focused with elegant and elaborate physical and mathematical techniques on the mechanical effects of mainly low-velocity air movements on filiform hairs, the response of the complex system of hair plus socket deserves a further quantification for the cricket.

The sensory activity of cercal filiform hairs has been shown to be involved in cricket behavior. They play a role in controlling particular escape reactions (Stabel et al. 1985; Gras and Hörner 1992), in detecting low-frequency components of sound generated near courting crickets (Kämper 1981; Kämper and Dambach 1985) and in the defensive "head-stand" response observed, for example, when *Acheta domesticus* is attacked by a female of the parasitic solitary digger wasp, *Liris niger* (Fig. 11.1) (Gnatzy and Heußlein 1986; Hustert and Gnatzy 1995; Gnatzy 2001).

Here we present data on the biomechanics of the coupling between filiform hairs and their sockets and on the physiology of the receptor cells of filiform hairs and campaniform sensilla, especially with respect to the effects of stimulus frequency and amplitude on the magnitude and phase of their response. Moreover we worked with a model system in which isolated, unfixed cerci of crickets (*G. bimaculatus* only) were set into a SEM and the hair shafts of individual filiform hairs were manually deflected in different directions. Strong deflection of the hair shaft parallel to the longitudinal axis of cercus causes tilting of the socket. Also, the sickle shaped area of thin cuticle around the large sockets of filiform hairs (with long hair shaft) was clearly indented as long as the socket was deflected toward the cercus tip. During a deflection toward the cercus base, however, it arched up.

11.2 Materials and Methods

11.2.1 Animals

Experiments were performed on adult *Acheta domesticus* L. and *Gryllus bimaculatus* Deg. (scanning electron microscopy only) from our own stock, at least 3 days after imaginal ecdysis.

11.2.2 Stimulation

Sinusoidal air movement was produced in a miniature wind tunnel, a Plexiglas cylinder with inside diameter 30 mm, by means of two bass loudspeakers (diameter 240 mm) in a push-pull arrangement. Pressure/suction tubes transmitted the air movement from the loudspeakers to the wind tunnel (Fig. 11.2a), in the middle of which the preparation and calibration sensors were positioned.

The loudspeakers were driven by a two-channel DC power amplifier rated at 100 watts per channel (continuous). A digital control unit connected to the amplifier allowed the stimulus to be varied systematically through 60 predetermined settings: six frequencies in the range 2–100 Hz (maximum error 1%), each at 10 amplitudes

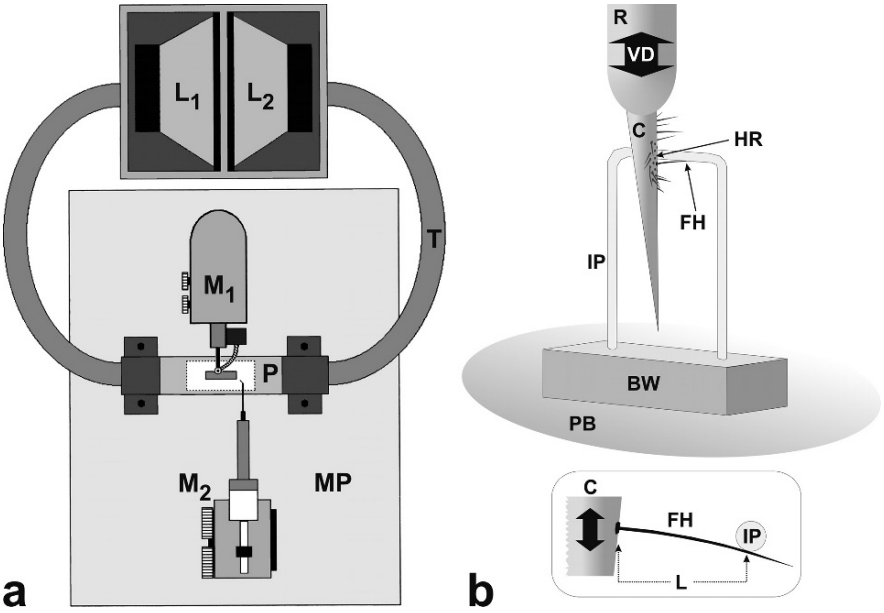

Fig. 11.2 **a** Experimental setup. A wooden box with two loudspeakers is connected to a Plexiglas cylinder by way of a pressure/suction tube. The cylinder is mounted on a metal plate, which also supports the micromanipulators for the recording electrode and the bimorph bender. **b** Measurement of force to bend a filiform hair. A cercus attached to a rod is vertically displaced by a micromanipulator. While surrounding hairs are removed from their sockets, one filiform hair is coupled to a bent insect pin stuck into a piece of balsa wood which rests on the pan of a balance. Most cercal hairs have been omitted for clarity. The *lower part* of the sketch shows the true proportions and the effective lever for force transduction. Balsa wood *BW*; cercus *C*; filiform hairs *FH*; surrounding hairs *HR*; insect pin *IP*; effective lever *L*; two loudspeakers *L1*, *L2*; micromanipulators *M1*, *M2*; Plexiglas cylinder *P*; metal plate *MP*; pan of a balance *PB*; rod *R*; pressure/suction tube *T*; vertical displacement *VD*

ranging from 5 to 5000 mm/s peak air velocity (maximum error 10%), both parameters being logarithmically spaced. For each stimulus the amplitude was increased linearly over two cycles, remained for one second at the calibrated level, and finally decreased over two cycles; during the pause between stimuli (ca. 5–10 s) the amplitude was attenuated by 60 dB. Then the next stimulus was started, at the next higher amplitude or frequency.

The apparatus was calibrated for frequency, amplitude and phase response with a laser anemometer (LDA 04; Dantec, Karlsruhe) that measured the wind velocity directly by means of smoke particles. The amplitude was calibrated between 3 mm/s and 3 m/s. Calibration values not measured were calculated by means of extrapolation from the measured values. The intrinsic resonant frequency of the wind tunnel was 6.5 Hz. The standard followed in the stimulus traces of subsequent histogram figures is that the descending part of the air-movement curve represented by a sinusoidal wave corresponds to deflection of the filiform hairs toward the tip of

the cercus, and the ascending part corresponds to movement that deflects the hairs toward the cercus base.

Using a piezo bimorph bender (PXE 5, 1.6 × 0.67 × 70 mm; Valvo, Hamburg), single hairs were reproducibly deflected. The bimorph bender was controlled by a trapezoidal-burst generator with a modified voltage amplifier. The frequency and amplitude responses of the bimorph bender were calibrated with a non-contact inductive displacement transducer (MultiVit KD Series 800 Micro Epsilon). The resonant frequency was 60 Hz. With trapezoidal stimuli the bender does not show post-ramp oscillations if the rise times are longer than 20 ms, up to a maximal deflection of 250 μm. With sinusoidal stimuli the oscillation amplitude of the bender was constant from 0 to 20 Hz. Because of the high voltages driving the bender (± 45 V), it was isolated from the preparation by attaching to it a thin-walled glass capillary with a fine insect pin fixed to its tip with dental wax.

11.2.3 Biomechanics

The oscillation angles of the filiform hairs were measured by visual inspection at specific sites along the hair shaft. A prerequisite for this procedure is that the hair shaft be quite rigid, so that it does not bend as it oscillates. Both our own pilot experiments and reports by Kämper and Kleindienst (1990, see Fig. 4a of that paper) indicate that this condition is fulfilled, at least as long as the hair is oscillating freely.

The cricket was immobilized by cooling (+5°C), decapitated and the hind legs and wings were removed. It was placed in the wind tunnel so that its longitudinal axis was parallel or transversal to the direction of air movement and its body was fixed in this position with wax. The cercus was viewed by reflected light with a stereo microscope (Wild M5) on which a CCD video camera (Sony JVC GX N7G) had been mounted. This apparatus was arranged in such a way that the direction of oscillation of the filiform hair to be measured was parallel to the plane of the CCD element. As the hair shaft was set in motion by air movement with preset combinations of frequency and amplitude (see above), its deflections were recorded. At the end of the test the shaft was torn out and its length was measured under a microscope.

The reversal points of the hair shaft's oscillatory movement were found by examining single frames of the video recording showing a blurred image of the entire arc swept out by a hair (image magnification up to 1:1200). The deflection angle was calculated as $\alpha = 2 \cdot \arctan(0.5 \cdot \text{oscillation amplitude} \cdot \text{hair length}^{-1})$. In addition, the movement itself could be followed in consecutive frames with sufficient temporal resolution when the stimulus frequency was 2 Hz. The measured values (at 6 frequencies and at 10 amplitudes: 60 values per experiment) were plotted as a 3D graphs with interpolated values (spline algorithm) for improved visualisation.

The degree of tilt of the hair socket was determined indirectly from the movement of the hair shaft, because direct measurement of the socket positions in the video picture was inadequate for quantitative analysis. Qualitative observations of

the socket movement served as a control, for deciding whether the socket was being tilted at a given air velocity and frequency.

The forces required to deflect a filiform hair or its socket were determined using a balance (Sartorius 4401, resolution 1 μg). A piece of balsa wood about 3 mm in length was placed on each of the two pans. An insect pin bent into an inverted U shape was stuck into each piece of wood. Cercal hairs surrounding the hair to be measured were removed, and the position of the cercus was adjusted under visual control until the hair, in its resting position, contacted the horizontal part of the insect pin (Fig. 11.2b). Then the cercus was moved vertically so that the force associated with deflection of the hair could be read as a loading or unloading of the balance pan. The effective lever arm (hair base to contact point on the hair) was measured visually.

11.2.4 Scanning Electron Microscopy

FESEM: A field-emission scanning electron microscope (FESEM, Hitachi Model S-4500) was used for representing cercal filiform hairs and campaniform sensilla. For this purpose adult crickets (*Acheta domesticus* and *Gryllus bimaculatus*) were anaesthetized with carbon dioxide. The excised cerci were prefixed for several hours in 2% glutaraldehyde (in 80 mM sodium-cacodylate buffer and 3.9% sucrose, pH 7.25), postfixed for 2 h in 2% OsO_4 in the same buffer, finally dehydrated in a graded acetone series. After critical-point drying in a Polaron unit, using CO_2 and amyl-acetate (2×15 min), the samples were glued to aluminum holders. Finally the specimen were gold coated in an Agar Sputter Coater, and then examined using the FESEM at an accelerating voltage of 1–5 kV. Images were recorded digitally. The pictures were processed with Adobe Photoshop software (Adobe Systems, San Josde, CA, USA).

SEM: The effects of manually controlled hair shaft deflection on the outer cuticular apparatus (i.e. hair shaft, socket etc.) of various filiform hairs coupled with campaniform sensilla could be observed continuously on a video screen of a SEM (Hitachi S 500). For this purpose adult crickets (*Gryllus bimaculatus*) were anesthetized with CO_2 and fixed with wax to a special block in such a way that the ventral surface of one of the two cerci rested on a modified SEM specimen holder (diameter 20 mm), where it was glued in position with Leit-C. As soon as the Leit-C had dried, the cercus was removed from the animal and the opening at the cut end was sealed with wax. The preparation was immediately inserted into the microscope column and observed at low acceleration voltage (5 kV). Using a piece of tungsten electrode wire mounted on the preparation plate so as to be flexible, individual filiform hairs (all with long hair shaft and large socket) accompanied by campaniform sensilla could be deflected in the SEM column in a controlled manner, both toward the tip and the base of the cercus. The elasticity of the cuticular structures was retained for ca. 10 min under high-vacuum conditions (2×10^{-4} torr) in the microscope column. Images were recorded on 35 mm film.

11.2.5 Electrophysiology

After the dissected cricket had been positioned in the wind tunnel, the cercus was placed on a wax support to minimize movement and oscillations induced by the air stimuli. A tungsten electrode was placed on the cercal surface near the hair socket, so that the activity of the receptors in the filiform hairs or campaniform sensilla was recorded through the cuticle. Care was taken to ensure that the equipment did not impede the movement of hair or socket.

Calibration data of the wind tunnel (air motion in response to electrical driving of the loudspeakers) were used to bring the extracellularly measured receptor-cell activity in correct temporal relation to the translation of air particles. Neuronal responses were digitized (sample rate: 40 kHz) and evaluated with a microcomputer.

To record from fibers in the terminal ganglion, which receives sensory input from the cercal mechanoreceptors, the abdomen was opened dorsally, intestine and gonads were removed and the ganglion was lifted on a silver support which also served as a reference electrode. A saturated aequous solution of cobalt hexamine chloride was injected, after electrophysiological experiments, by direct current (5 nA) from glass microelectrodes, precipitated with $(NH_4)_2S_2$ and intensified following standard protocols. Preparations were sketched with the help of a camera lucida attached to a light microscope.

11.3 Results

Crickets have, at the rear end of their abdomen, conspicuous, paired, cone-shaped cerci (reaching a length of about 5 mm in adults of *Acheta domesticus*), bearing five different types of sensilla, e.g. filiform hairs and campaniform sensilla. Scanning micrographs show that the hair shaft of all filiform hair is situated in a cuticular socket (Fig. 11.3). The shaft of these hairs varies in length from ca. 30 μm up to 1.5 mm (in *Acheta domesticus*) and 3 mm (in *Gryllus bimaculatus*). In *G. bimaculatus* ca. 250 filiform hairs with shafts longer than ca. 150 μm are flanked by campaniform sensilla. Only the sockets of those filiform hairs are surrounded by a sickle shaped area of cuticle, which connects the base of the sockets with the remaining cercus cuticle (Fig. 11.3b). As earlier studies have shown (Dumpert and Gnatzy 1977) this thin smooth cuticle (thickness 0.5 μm; surrounding cercus cuticle ca. 7 μm) has a larger extension (about 10 μm) in direction of the tip of the cercus. All sockets surrounded by such a sickle shaped area of cuticle can be bent in direction of its largest extension (max. 30°, to tip of the cercus). Towards the cercus base the maximum bending angle is 18°. Perpendicular to this tilt axis the sockets can only be deflected by about 3°. Upon release deflected sockets immediately return to their undeflected position. The specific geometry of cuticular elements with individual mechanical properties is fundamental to the transfer function of filiform hair receptors and campaniform sensilla as studied in this work.

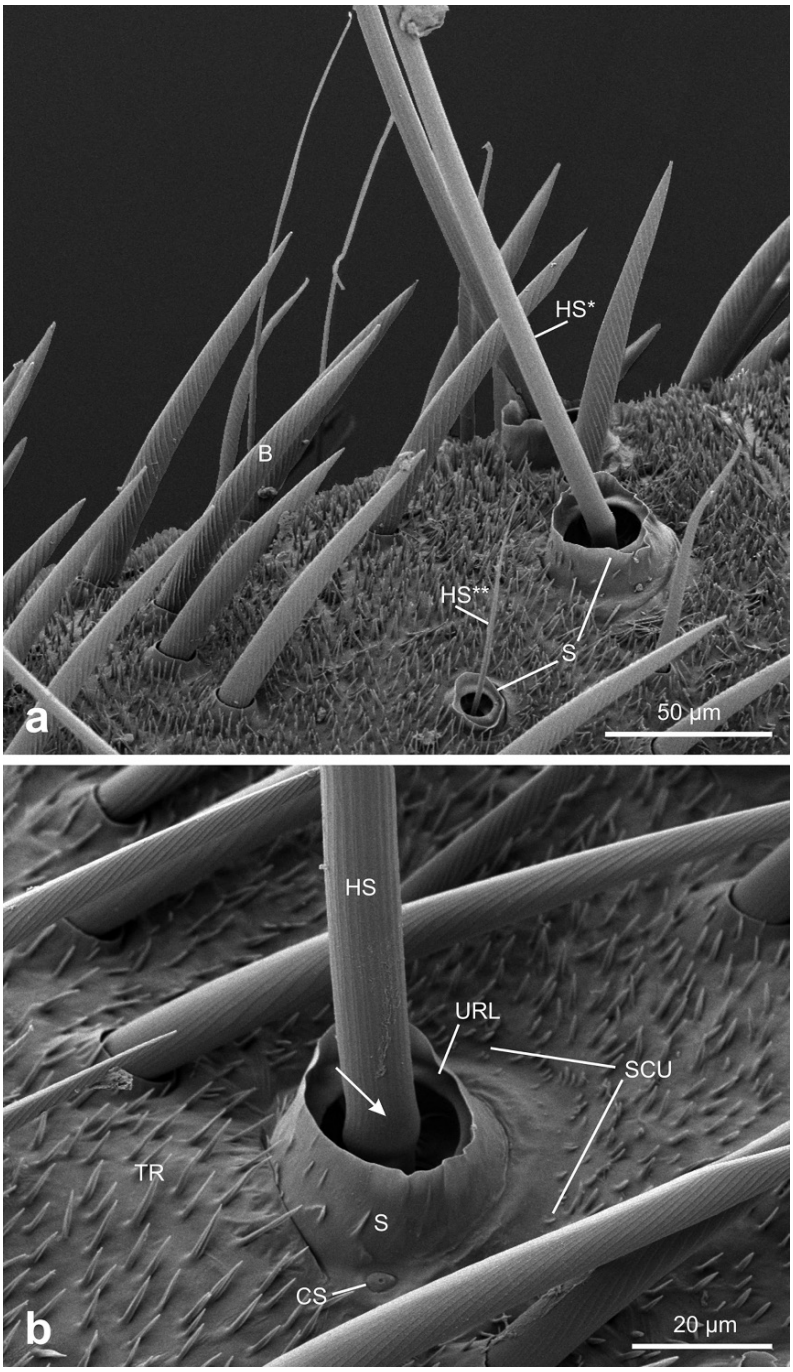

Fig. 11.3 (continued)

11.3.1 Mechanics of Filiform-Hair Movement

Figure 11.4 illustrates the oscillation, in air moving sinusoidally at 2 Hz, of a filiform, type L hair (shaft oscillation direction parallel to the long axis of the cercus; shaft length 1200 μm). When the stimulus amplitude is small (up to 100 mm/s air velocity) the hair movement closely follows that of the air and hence is sinusoidal. With increasing stimulus intensity the angular deflection increases (the absolute value depends on the length of the hair shaft; see below). Once the air velocity exceeds 0.5 m/s, an increase in stimulus intensity at first causes no increase in maximal oscillation amplitude, because the hair shaft strikes the socket and is not deflected further. The socket shape is asymmetric, limiting the angle of free hair oscillation to about 7° toward the tip of the cercus and only 4° toward its base. These values are similar for all types of filiform hair, and are largely independent of shaft length. The total angle for free shaft movement is at most 14° and usually around 10°–12° (n=24).

The preferred direction of the socket tilt is always parallel to the long axis of the cercus (Dumpert and Gnatzy 1977). In the example shown in Fig. 11.4 an air velocity of 5 m/s is required for the socket to be tilted. When the socket begins to move along with the hair, there is a marked increase in the amplitude of hair oscillation, accompanied by a distinctly greater asymmetry of the oscillation about the resting position. That is, the increase in amplitude is about twice as great toward the tip of the cercus as toward the base.

The oscillation angles of filiform hairs of various lengths are diagrammed as a function of velocity and frequency of air oscillation, for L-hairs in Fig. 11.5 and for T-hairs (preferred direction transverse) in Fig. 11.6. At air velocities > 5 mm/s, long filiform hairs (shaft longer than 1000 μm) oscillate over larger angles than shorter hairs. Therefore the shafts of larger hairs begin to strike the socket at stimulus intensities (ca. 200 mm/s) at which the smaller hairs are still oscillating freely. Within a certain range of higher intensities the socket does not tilt and hence restricts the movement of the hair (see Fig. 11.4); in this range, changes in stimulus amplitude cannot be discriminated on the basis of the oscillation angle of the hair shaft. Not until the air velocity increases by a factor of ten does the oscillation amplitude

Fig. 11.3 FESEM micrographs of cercal filiform hairs and campaniform sensilla of two cricket species. **a** *Gryllus bimaculatus*: Low magnification micrograph of cercus surface showing a filiform hair with long hair shaft *HS** inserting in a large and a filiform hair with very short hair shaft *HS*** inserting in a small cuticular socket. Note that the larger the socket the smaller is the relative distance between hair shaft and upper ring lamella of the socket. **b** *Acheta domesticus*: High-magnification micrograph of a large socket of a filiform hair (with long hair shaft) and one campaniform sensillum. Note that the socket is surrounded by a area of smooth cuticle. This sickle shaped area of cuticle (looking like a "halo") can clearly be recognized as there are no trichomes as on all other parts of the cercus surface. Sockets of this type of filiform hairs, i.e. with long hair shaft, can be bent farthest in the direction of largest extension of the "halo", i.e. toward the cercus tip. Bristle hairs *B*; campaniform sensillum *CS*; hair shaft *HS*; cuticular socket *S*; area of smooth cuticle *SCU*; trichomes *TR*; upper ring lamella *URL*; thickening of hair shaft *arrow*

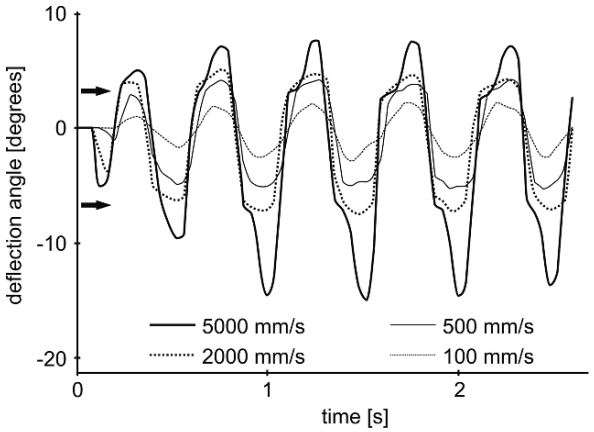

Fig. 11.4 Deflection of a 1200-μm-long L-filiform hair during sinusoidal air movement. The deflection angle was measured visually with a temporal resolution of 0.04 s. Negative angles represent deflection of the hair shaft toward the tip of the cercus and positive angles, deflection toward the base. The values connected by a continuous *heavy* line were measured at 5000 mm/s air velocity. The *dashed* and *light lines* show the hair movement for stimulus intensities of 2000, 500 and 100 mm/s, respectively. The deflections beyond which the hair shaft is in contact with the upper ring lamella of the socket are indicated by *arrows*

suddenly increase, as the socket and hair begin to oscillate together. Both T- and L-hairs exhibit a pronounced peak at frequencies of 10–20 Hz, regardless of hair length (length increases from a to f in Figs. 11.5 and 11.6). Furthermore, in this frequency range the socket ceases to be stable at considerably lower air velocities than when the frequency is 2 or 100 Hz; that is, the force required to tilt the socket is lower in the 10- to 20-Hz range.

The sockets of both L-hairs and T-hairs all tilt in the same direction, parallel to the long axis of the cercus (Dumpert and Gnatzy 1977). In the case of T-hairs, therefore, the plane in which the hair oscillates together with the socket is perpendicular to the preferred direction of hair oscillation. In the range of amplitudes tested here (max. 5 m/s), air movement parallel to the preferred oscillation direction of the T-hairs (that is, transverse to the long axis of the cercus) never caused the hair shaft to tilt the socket (Fig. 11.6a–f). Hence there is a particular air velocity – ca. 200 mm/s, depending on the length of the hair shaft (as in the case of the L-hairs) – beyond which the oscillation amplitude of the hair does not increase. Air movement parallel to the long axis of cercus produces little or no movement of the T hairs in that direction at low intensities, but at ca. 1 m/s or more a component of hair shaft oscillation appears which is due to tilting of the socket (Fig. 11.7a–d). At these intensities the hair shaft oscillates in a direction transverse to the cercus, even when the driving air movement is rotated by 90° from this preferred direction of oscillation.

Short filiform hairs (< 500 μm) respond considerably less strongly to stimuli in the lower frequency range than to those at higher frequencies (Fig. 11.5a–c). Given a constant air peak velocity (100 or 200 mm/s) such that the hair shaft oscillates freely, at 2 Hz a hair is deflected over an angle only about one-fifth as large as at 100 Hz. On average, the oscillation amplitude of small hairs increases by ca.

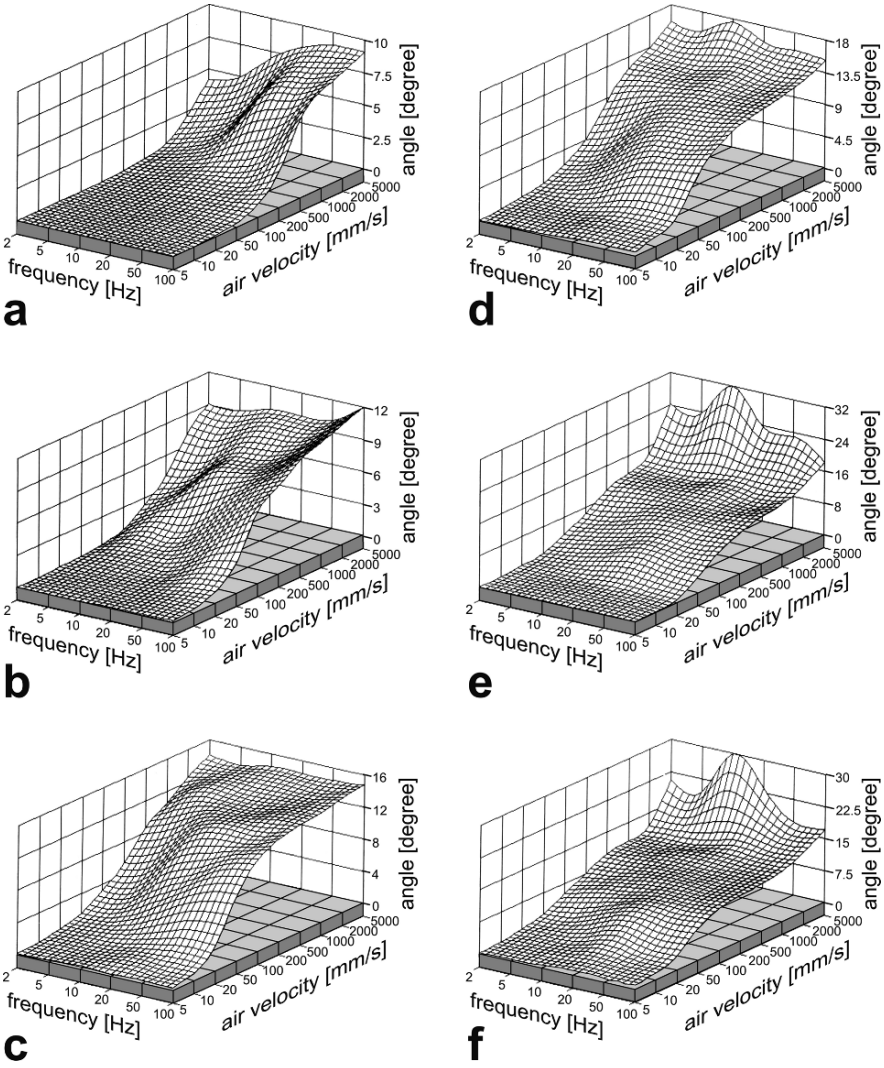

Fig. 11.5 Oscillatory characteristics of L-filiform hairs. The deflection of hairs oscillating parallel to the long axis of the cercus was measured in the plane of oscillation by visual inspection. Length of the filiform hairs: **a** 110 μm, **b** 270 μm, **c** 480 μm, **d** 710 μm, **e** 1200 μm, **f** 1300 μm. The measured angles are plotted upward (notice different scaling), above the grid formed by the stimulus-frequency and air-velocity coordinates. The frequency increases logarithmically from left to right, and the stimulus intensity increases logarithmically from front to back. The graphs show that as the hair length increases, the frequency response becomes flatter and the sensitivity rises. The plateau in the upper amplitude range, visible in **c–f**, is due to the hair shaft striking the ring lamella of the socket

10 dB per frequency decade (9.5 dB, average of 20 measurements on 5 hairs). Air velocities below 100 mm/s were not included in these calculations, because in this range (particularly for small filiform hairs) the deflection angle was at the measurement technique's limit of resolution. Long filiform hairs (> 1000 μm) have a flatter

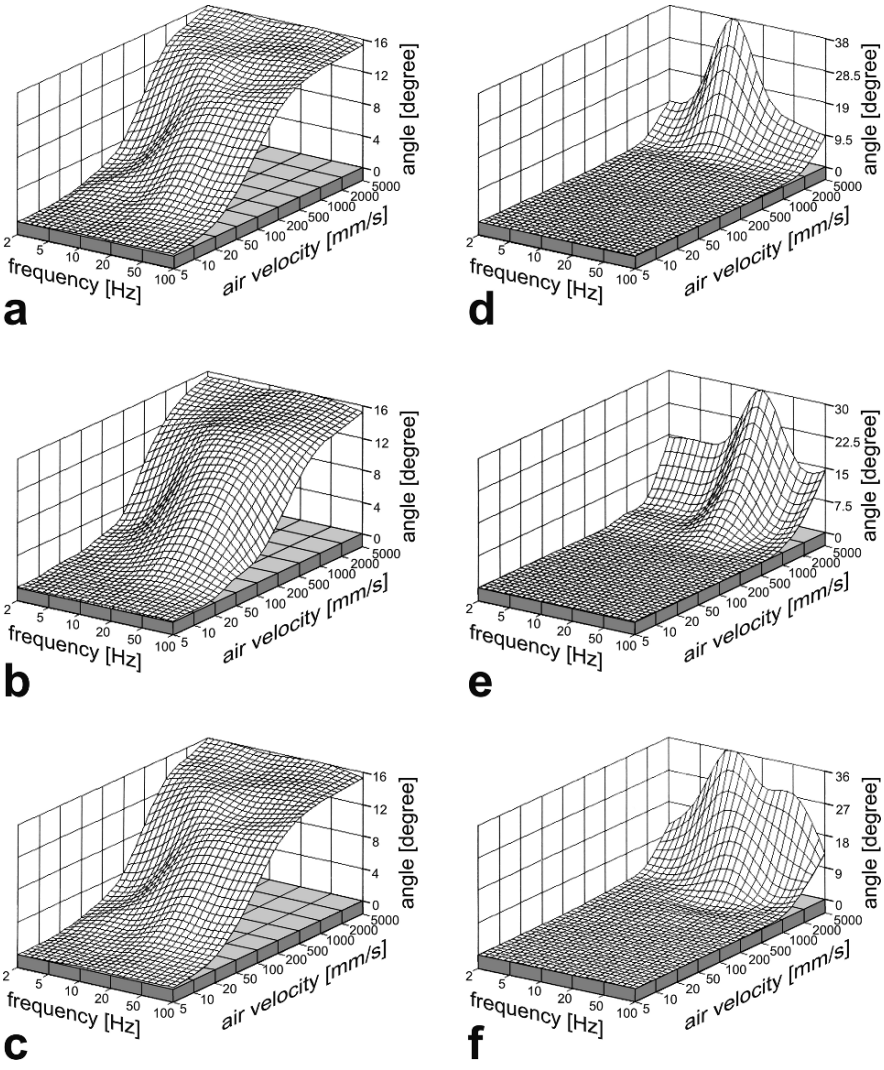

Fig. 11.6 Oscillatory characteristics of T-filiform hairs. **a–c** Deflection transverse to the long axis of the cercus. Length of hair: **a** 300 μm, **b** 740 μm, **c** 835 μm. The graphs show the restriction of hair movement in the upper amplitude range, which appears at an oscillation angle of about 14° regardless of hair length. **d–f** Deflection parallel to the long axis of the cercus. Length of hair: **d** 840 μm, **e** 1030 μm, **f** 1250 μm. The graphs show the component of the hair oscillation produced by tilting of the hair socket in the long direction of the cercus. The lowest thresholds, 500 mm/s air velocity, are associated with the oscillatory resonance at 10–20 Hz. Note different scaling of vertical axis for **a**–**c**, **d**, **e** and **f**

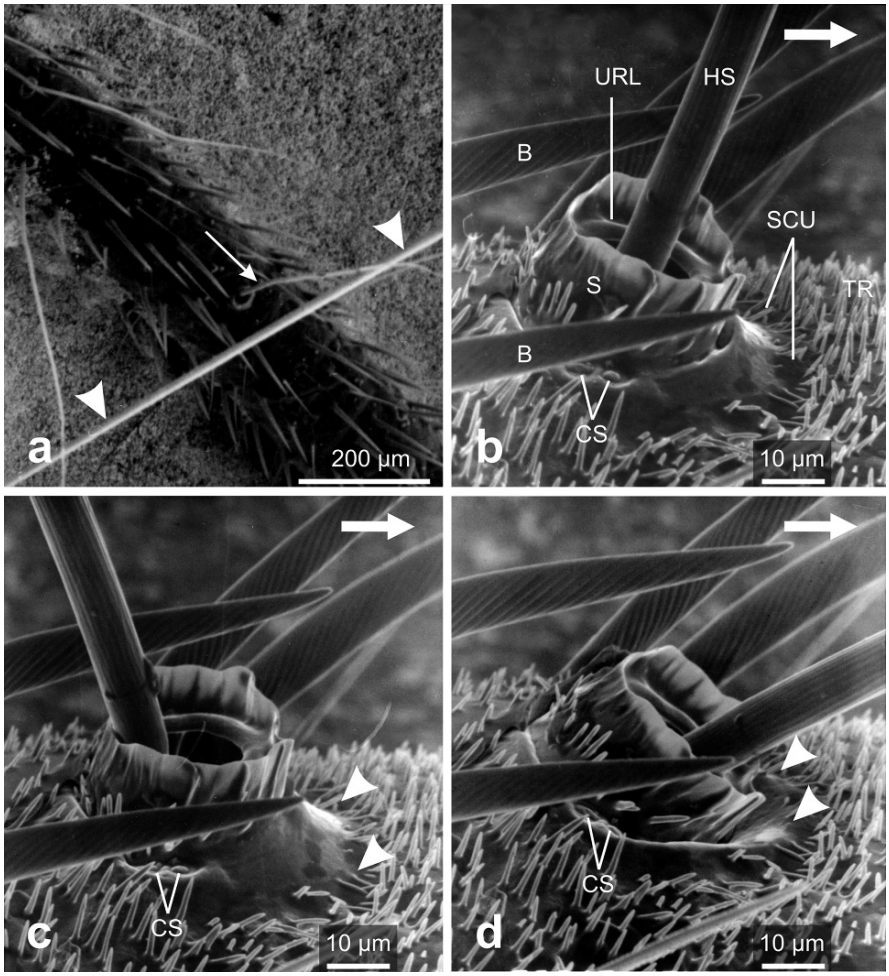

Fig. 11.7 Scanning electron micrographs showing test arrangement and changes in the cuticular apparatus of one and the same cercal filiform hair of a cricket (*Gryllus bimaculatus*) during deflection of whose long hair shaft. **a** Low magnification SEM showing part of a cercus glued on a SEM specimen holder. Note filiform hair *arrow* which is manually deflected (by a piece of a movably mounted tungsten electrode wire) *arrowheads.* **b** Side view of a filiform hair in resting position. **c** Side view of the same filiform hair (cp. with **b**) with long hair shaft. Note that the area of smooth cuticle surrounding the socket is arched *arrowheads* if the socket is bent toward the cercus base by the hair shaft. **d** Side view of the same hair as in **b** and **c**, tilted so as to deflect the socket toward the cercus tip. Note that now the smooth sickle shaped area of cuticle around the socket is deeply indented *arrowheads*. *White arrow* in **b**–**d** points toward the cercus tip. Tips of bristle hairs *B*; campaniform sensilla *CS*; hair shaft *HS*; cuticular socket *S* with upper ring lamella *URL*; sickle shaped area of smooth cuticle *SCU*

frequency-response characteristic (Fig. 11.5e, f), increasing only slightly from 2 to 10 Hz (ca. 5 dB/decade) and hardly at all from 20 to 100 Hz. Hairs of intermediate length have intermediate characteristics (Fig. 11.5d).

In the range of air velocities around 50–100 mm/s a small increase in the oscillation amplitude of both L-hairs (Fig. 11.5d–f) and T-hairs (Fig. 11.6a–c) can be discerned at 50 Hz. The frequencies tested were too widely spaced (2, 5, 10, 20, 50, 100 Hz) for any detailed conclusions to be drawn about the resonant frequencies of filiform hairs.

The movement of the hair shaft within the socket is limited to about 10°–12° total deflection angle, regardless of the type of hair (cf. Figs. 11.5 and 11.6); angles as large as 30° are found for the oscillation of a hair together with its socket. At a given air velocity, the socket tilts further toward the tip of the cercus than toward its base. Dumpert and Gnatzy (1977) ascribed this phenomenon to the asymmetric structure of the "joint membrane" surrounding the socket (see also Fig. 11.7b–d). Direct measurements of the hair (Fig. 11.8) have shown that the force required to tilt the socket from its resting position toward the tip of the cercus is smaller than that for the opposite direction of tilt. This effect is noticeable when the hair shaft is

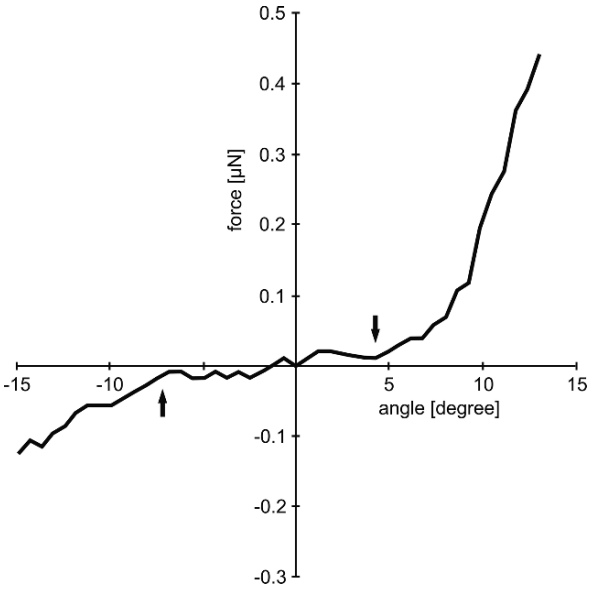

Fig. 11.8 Forces acting at the shaft of a 1200-µm-long filiform hair when the socket is tilted toward the base of the cercus (positive angles) or toward its tip (negative angles). The hair shaft was coupled to a precision balance at a point 870 µm from the base and displaced vertically in 10-µm steps. The force read off at the balance, in µg, was converted to µN on the basis of an effective lever arm 1000 µm in length. The measured forces are plotted as a function of the calculated deflection angle. Positive forces are defined as those opposing deflection of the hair toward the base of the cercus (that is, forces directed toward the tip of the cercus). The angles at which the shaft strikes the socket are indicated by *arrows*

deflected by more than about 8° from its resting position, because it is in this range of angles that the socket begins to be tilted. For a 10° deflection of the shaft in both directions, the ratio of the forces acting on the shaft is about 2:1. For larger angles, the force opposing deflection toward the base of the cercus rapidly increases; the socket cannot be tilted more than ca. 15° in this direction, so that additional force causes the hair shaft to bend.

11.3.2 Mechanics of the Cuticular Socket

Observations of socket movement in the light microscope confirmed the threshold angles for tilt measured at various frequencies and provided further evidence that the reasons for the asymmetry of hair movement reside in the morphology of the socket. Measurements of scanning electron micrographs showed that in the resting position the distance from the hair shaft to the upper ring lamella of the socket is about 1/3 larger toward the tip than toward the base of the cercus (Table 11.1). This ratio is about the same as the ratio of the angles through which the shaft can be deflected, proximally or distally, until it strikes the upper ring lamella of the socket. The effect of the asymmetric position of the hair shaft with respect to the socket is enhanced by a structural nonuniformity of the shaft itself, a thickening on the side toward the base of the cercus, at the level of the upper ring lamella of the socket (cf. Fig. 1d, Dumpert and Gnatzy 1977). These morphological features are evidently responsible for the fact that, at high stimulus amplitudes, the hair shaft within the socket can oscillate further toward the tip of the cercus than toward its base.

To find out what happens at the cuticular apparatus of such a cercal combined mechanoreceptor (i.e. filiform hair and campaniform sensilla) we worked with a model system using a SEM to get a higher resolution. In doing so we set unfixed cricket cerci into a SEM column and used a movable tungsten wire for controlled bending of a single hair (Fig. 11.7a). Thereby we were able to observe that the sickle shaped area of smooth cuticle around the socket of a filiform hair was indented as long as the socket was deflected in the direction toward the cercus tip. During a deflection of the same filiform hair toward the cercus base, however, it bulges

Table 11.1 Hair-shaft and socket geometry as measured in 12 long filiform hairs, each with 3 campaniform sensilla having dimensions $2.8 \pm 0.8 \times 3.7 \pm 1.2\,\mu m$

Measured distance	Arithmetic mean ± standard deviation (μm)
Diameter of hair shaft	9.8 ± 0.4
Diameter of hair socket	26.3 ± 1,5
Diameter of upper ring lamella in long direction of cercus	19.2 ± 1.6
Diameter of upper ring lamella transverse to the cercus	17.0 ± 1.3
Distance between hair shaft and upper ring lamella in direction toward base of circus	3.6 ± 1.0
Distance between hair shaft and upper ring lamella in direction toward tip of circus	5.9 ± 0.8

upward (Fig. 11.7b–d). The resulting displacements of the cuticle (< 1 μm) may be sufficient to stimulate the campaniform sensilla adequately.

11.3.3 Physiology of Filiform Hairs

To supplement the previous findings regarding the sensory apparatus and mechanisms of stimulus transduction (Gnatzy and Tautz 1980) and the physiology of the sensory cells in the threshold region (Shimozawa and Kanou 1984b) or at single pulse stimulation (Landolfa and Miller 1995), we investigated the responses of the sensory cells in L-hairs to sinusoidal air movement at various frequencies and intensities. The lowest air velocity available through our experimental setup, 5 mm/s, was above the threshold of *very long filiform hairs* (shaft length > 1000 μm; Fig. 11.9a); here the threshold is statistically defined, because the receptors in such hairs always have a certain background activity.

Long filiform hairs (ca. 700–1000 μm) do not encode stimulus intensity in their discharge rate over the entire range of intensities tested; in fact, at high air velocities the number of spikes discharged is actually reduced. *Short filiform hairs* (< ca. 700 μm) are less sensitive than long hairs. The frequency-dependence of their oscillation angle, observed in biomechanical measurements, is reflected in the responses of the sensory cells (Fig. 11.9b). For a stimulus at 2 Hz to be detected, the air velocity must be about 10 times higher as at 20 Hz. The dependence of threshold on frequency could not be determined for all frequencies, because the hairs were too sensitive in the high-frequency range (thresholds below 5 mm/s could not be measured with the apparatus). With the threshold response defined as more than altogether 3 spikes in the same phase relation to the sinusoidal air movement during a 1-s stimulus (single stimulus-correlated spikes were discharged during lower-intensity stimuli), in the lower frequency range the threshold fell (i.e., sensitivity rose) by ca. 20 dB per frequency decade. The number of spikes discharged by small filiform hairs is clearly dependent on stimulus intensity over the range of air velocities tested (Fig. 11.10). The variability of spike size in the example illustrated indicates that at high stimulus intensities the electrode is also set into oscillation. To determine whether the recorded activity derived from one or more sensory units, the hair under observation was immobilized during the air movement or deflected individually, in the absence of air movement, by a piezo bimorph bender.

Fig. 11.9 Responses of filiform hairs to sinusoidal air movement. **a** 1300-μm hair. PST* histograms for consecutive stimuli at 2 Hz with air velocity increasing logarithmically from 0.5 to 5000 mm/s (*top to bottom*). The stimulus onset is marked by a small triangle in each case. **b** 400-μm hair: PST histograms for consecutive stimuli at 5 Hz. The stimulus trace represents the actual translation of the air particles. * Peristimulus time (PST) histograms display the distribution of spike times relative to the onset of each stimulus presentation

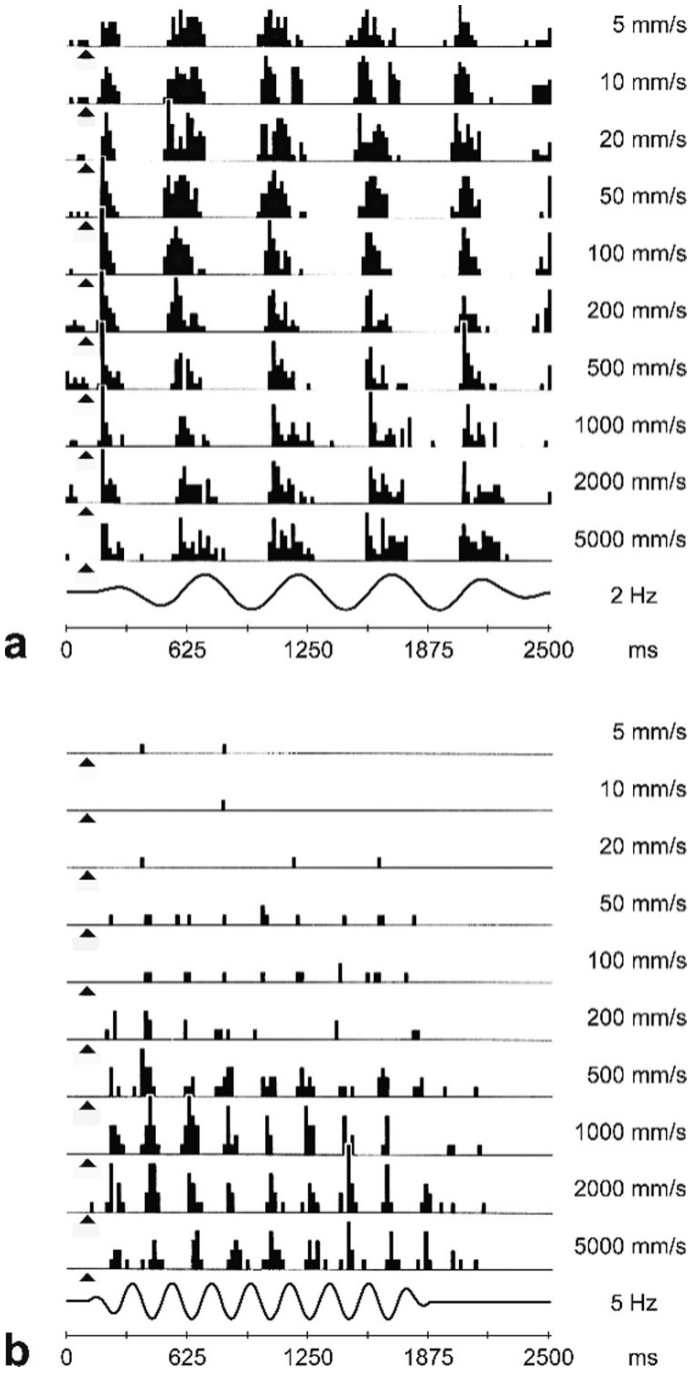

Fig. 11.9 (continued)

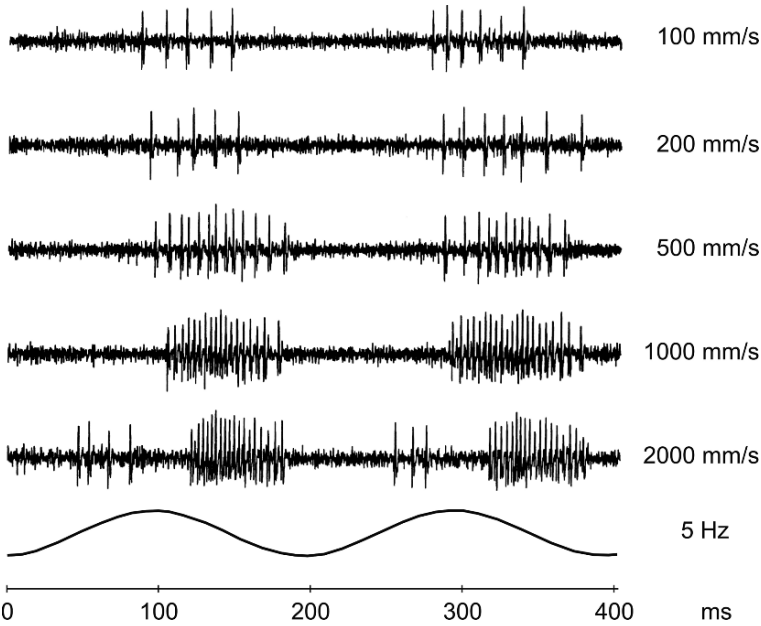

Fig. 11.10 Original recording from a filiform hair 500 μm in length stimulated with 5-Hz at intensities increasing from *top* to *bottom*: 100, 200, 500, 1000 and 2000 mm/s air velocity. The discharge of the receptor cell – for each given velocity – is related to a certain phase of the stimulus, and the number of spikes rises with increasing stimulus intensity. The recording also illustrates the problem that the amplitude of the potentials varies due to oscillations of the whole cercus and of the electrode that are induced by high-intensity stimuli. The stimulus trace represents the actual translation of the air particles

The intervals between the action potentials in the response of small filiform hairs, as in the case of larger hairs, varied as a function of stimulus intensity. With increasing air velocity the interspike interval first fell to less than 2 ms, but from a certain velocity on, a further increase in stimulus intensity was accompanied by a decrease in discharge rate (i.e. longer intervals). Usually the maximal discharge rate of sensory cells in short filiform hairs (up to ca. 600 μm) was reached at air velocities around 1 m/s, in the lower part of the frequency range tested (2, 5, 10 Hz). At higher frequencies (20, 50, 100 Hz) this maximum was shifted to lower stimulus intensities (ca. 200 mm/s; Fig. 11.11). The data pooled from low as well as from high frequency stimulation follow log-normal distributions (χ^2 test, $p<0.05$, dashed lines in Fig. 11.11) with nearly identical standard deviations. This indicates that the overall variability and dynamic of the sensory response remains constant over a broad range of stimulus frequencies, but becomes adjusted to different air velocities. By deflecting the hair shafts directly with the bimorph bender, it was shown that the discharge of the sensory cells of long hairs during the initial movement is reduced after a certain position has been reached – evidently the position at which the socket begins to be tilted.

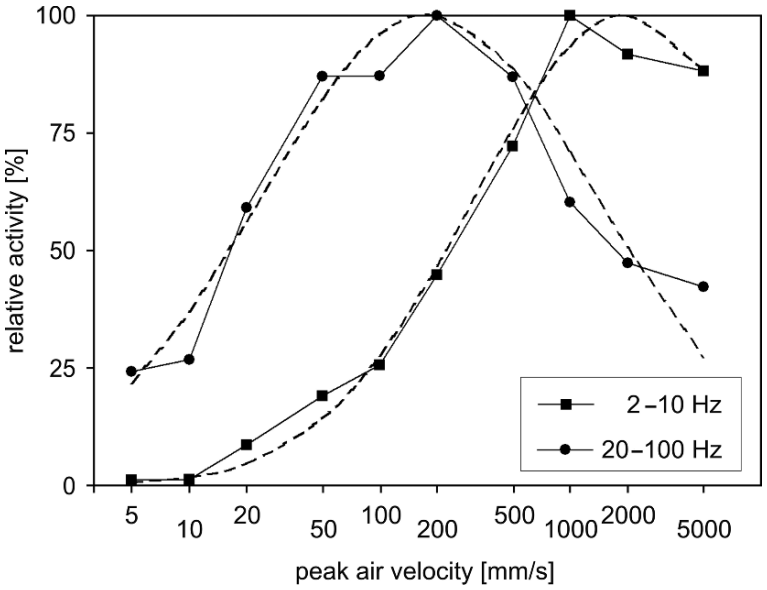

Fig. 11.11 Stimulus-intensity-dependent activity of a filiform hair 500 μm long. The values are normalized with respect to the maximal spike activity; values are pooled for low frequencies (2, 5, 10 Hz) and high-frequencies (20, 50, 100 Hz). The *dashed lines* indicate log-normal distributions fitted to the two data sets by non-linear least squares regression

11.3.4 Physiology of Campaniform Sensilla

The responses of individual campaniform sensilla to tilting of the socket, recorded extracellularly through the cuticle of the cercus, were all fairly similar to one another, as were the resulting displacements of the membranous cuticle. As the socket was tilted by direct contact, the number of spikes generated by the sensory cells depended on the speed of socket movement; when the deflection velocity was kept constant, an additional influence of the degree of socket tilt on discharge rate became apparent (Fig. 11.12). The spike activity usually subsided when the socket was held steady at a particular angle. However, some of these sensilla exhibited a more tonic response characteristic, continuing to discharge (though at a reduced rate) when the socket was held in a tilted position.

Most of the campaniform sensilla from which extracellular recordings were obtained were responsive to sinusoidal air movement in the range 2–100 Hz at velocities of more than 500 mm/s. This behavior is consistent with the results of the biomechanical measurements (see Discussion). The activity decreased very little even during prolonged (1 s) stimulation (Fig. 11.13a). The phase lag of these responses was typically reduced as stimulus intensity increased (Fig. 11.13b, c).

The number of action potentials depended on stimulus frequency and air velocity. Most campaniform sensilla showed the greatest sensitivity at frequencies near

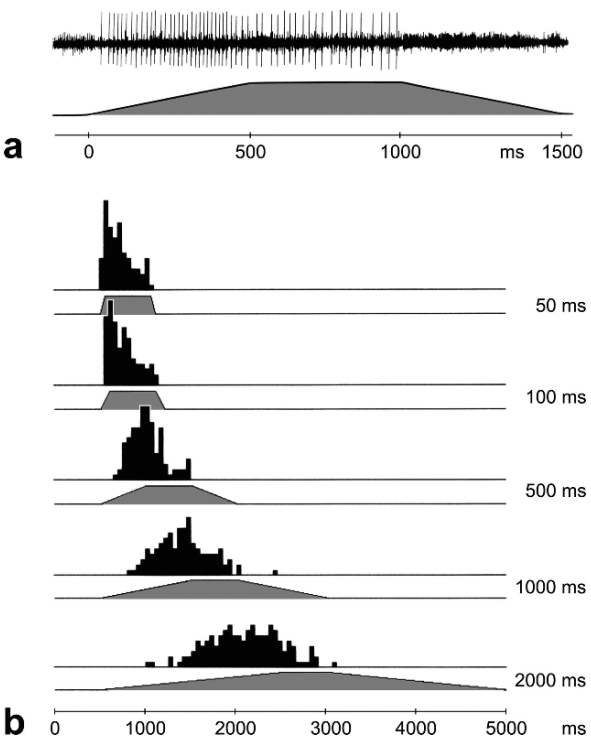

Fig. 11.12 Responses of campaniform sensilla to tactile stimulation of the filiform hair. **a** Original recording of the spike activity of the receptor cell in a campaniform sensillum after tactile displacement of the hair shaft. The stimulus time course is shown below the recording; the rise time was 0.5 s and the overall stimulus lasted 1.5 s. When the hair shaft is maximally deflected, the receptor cell of the campaniform sensillum remains active, although the socket is not being tilted any further (top of the trapezoidal stimulus). **b** Single response PST histograms for tactile stimuli with rise times varying from 50 to 2000 ms (50 time bins each 50 ms wide, max. 17 spikes per bin). The time course of the trapezoidal stimulus is shown below each histogram

20 Hz, responding to stimuli at velocities as low as 500 mm/s. At the other frequencies, the thresholds were in the region of 1 m/s; at 2 Hz campaniform sensilla often did not respond until the air velocity was raised to 2 m/s. Discharge rate was often maximal at 50 Hz and 5 m/s (Fig. 11.14). However, the number of campaniform sensilla for which extracellular recordings were available was not large enough (n=15) for a correlation to be established between the slight differences in their responses and the biomechanical characteristics of the various types of associated filiform hairs.

As the tungsten electrode was in direct contact to the filiform hair socket, it might mechanically affect the response characteristic of the campaniform sensillum, e.g.

Fig. 11.13 Responses of campaniform sensilla to sinusoidal air movement. **a** PST histogram of the activity of a campaniform sensillum during stimulation at 10 Hz with 2000 and 5000 mm/s air velocity; bin width 20 ms, 100 bins, max. 4 spikes per bin. **b, c** Phase of the spike activity of campaniform sensilla with respect to the sinusoidal air movement at **b** 5 Hz and **c** 20 Hz. The air velocity increases from top to bottom. Spikes first appear at 1 m/s, and as the stimulus intensity increases further, the discharge begins earlier in the cycle of air particle movement bending the filiform hair to the cercus tip

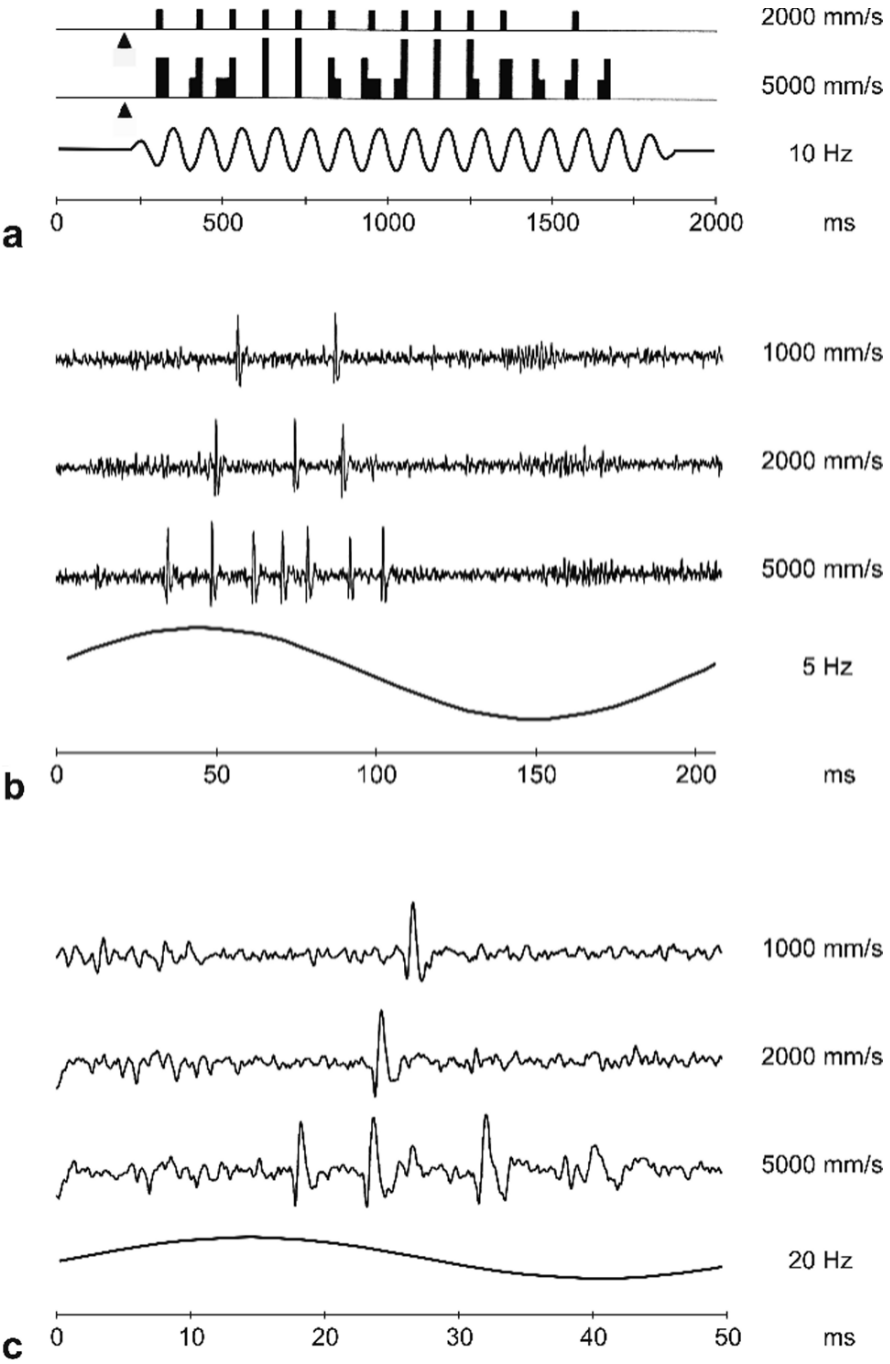

Fig. 11.13 (continued)

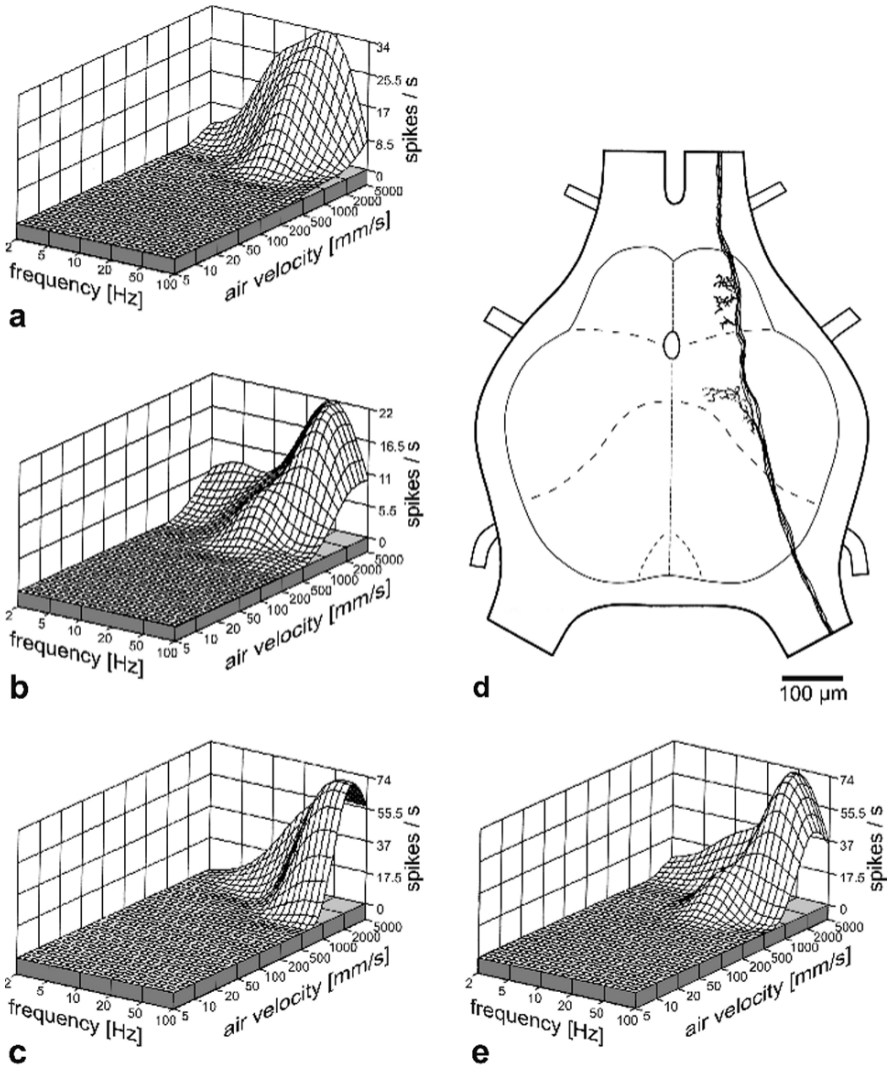

Fig. 11.14 Response characteristic of campaniform sensilla. **a–c** Extracellular recording with electrode on the cercal cuticle. The distinctive features of the campaniform sensilla of filiform hairs are the high thresholds (ca. 1000 mm/s) for stimulation with sinusoidal air signals and the typical frequency-dependence of the responses. Several types of response behavior are clearly distinguishable; the most common (60%) were of the type illustrated in the middle graph. **d, e** Quasi-intracellular recording in the terminal ganglion. **d** The cobalt hexamine chloride released from the recording electrode stained four parallel axons of campaniform sensilla. The terminal projections lie in the 6th abdominal ganglion. **e** The recorded activity corresponds to the most common type of response characteristic. In this situation, an influence of the recording apparatus on the filiform hair, and hence indirectly on the response characteristic of the campaniform sensillum, is excluded

by deformation of the cuticule. To exclude those artefacts, we inserted a microelectrode into the terminal ganglion to record from the axonal fibres of the sensory cells at the level of neuromer 7 to avoid recording from filiform hair afferences. As the tightly packed axons of campaniform sensilla have extremely small diameters, the microelectrode simultaneously penetrated more than one fibre in the experiment shown in Fig. 11.14d, e. This resulted in the diffusion of cobalt hexamine chloride into some neighbouring axons (Fig. 11.14d), which exhibit the typical projections of campaniform sensilla in the anterior neuromeres of the terminal ganglion (cf. Heusslein and Gnatzy 1987). However, since all spikes in the analyzed record were of uniform size and duration, they probably derived from one single sensillum. The frequency-amplitude response field determined from this experiment (Fig. 11.14e) corresponds very closely to the average characteristic obtained by extracellular recording (Fig. 11.14a–c) and, therefore, corroborates these results.

11.4 Discussion

11.4.1 Choice of Stimulus Parameters

The cercal filiform hairs of crickets had been known to respond to minimal air-particle movements (less than 0.1 mm/s; Shimozawa and Kanou 1984a). The campaniform sensilla coupled with the filiform hairs require stronger stimuli, such as air pulses of about 2 m/s or more, to cause the hair shaft to deflect the socket (Dumpert and Gnatzy 1977). The stimuli in our experiments, sinusoidal air-particle movements (2–100 Hz, 5–5000 mm/s air-particle velocity) under near-field conditions (Markl 1973; Tautz 1979), thus included the interesting transition region for the mechanical coupling of hairs and campaniform sensilla, at air velocities around 1 m/s.

11.4.2 Mechanics

According to the mechanical measurements, the long filiform hairs have no marked frequency-dependence in the range 2–100 Hz, with air velocity constant. Their oscillation angle is approximately doubled as the frequency rises from 2 to 10 Hz but remains about the same from 20 to 100 Hz. They also show hardly any sign of resonance. The oscillation amplitude of the short hairs, on the other hand, gradually rises over the entire frequency range tested, by ca. 10 dB per frequency decade. The oscillation angle triples when the frequency is increased tenfold. On the basis of theoretical considerations and measurements of the hair suspension's spring stiffness, Shimozawa and Kanou (1984b) calculated the frequency responses of filiform hairs 100–1000 μm in length, for the stimulus intensity range 0.1–100 mm/s (see Fig. 5a of Shimozawa and Kanou 1984b). Their results are in close agreement with our measured data. Shimozawa and Kanou calculated the angular displacement of four hairs differing in length, in the frequency range 1–1000 Hz, and compared these

theoretical values with the results of measuring 6 hairs at 50 Hz and 10–100 mm/s air velocity. They found the frequency response of the longest hair to be relatively flat, with maximal oscillation amplitude at 100–200 Hz (depending on the air velocity). The frequency response curve of short hairs was found to go up by 10 dB per frequency decade. For sinusoidal air movement at 100 mm/s and 100 Hz, Shimozawa and Kanou (1984b) calculated a deflection angle of 9° for a long hair and 1.3° for a short hair (derived from Fig. 5a, Shimozawa and Kanou 1984b). Our own measurements of hairs of comparable length gave results of the same order of magnitude: 10° for a 1200-μm hair and 2° for a 110-μm hair.

With a method similar to ours, Kämper and Kleindienst (1990), using detailed measurements, have shown data on the frequency response of filiform hairs directly comparable to our own. They showed that with a constant stimulus amplitude, 5 mm/s peak air velocity, the deflection angle of the hairs increases with increasing frequency, by 0–6 dB/octave (= 0–20 dB/decade) from 10 Hz up to their best frequency, between 40 and 100 Hz. The response curve of a short (500 μm) filiform hair rises by ca. 11 dB/decade, and that of a long (1300 μm) hair by ca. 6 dB/decade. Again, the results are basically consistent with our own measurements, in that Kämper and Kleindienst also found a steeper slope for shorter hairs. The slight differences in the values can be explained not only by the possibility of natural variability in the oscillatory parameters of filiform hairs (the mechanical properties of the cuticular hair suspension depending on various parameters such as the age of the animals, the humidity and the temperature) but also by the fact that our data were obtained at six distinct frequencies in the range of 2–100 Hz and not with a tuned frequency band. In Figs. 11.5 and 11.6, for example, it is evident that the hairs responses do not change completely linearly over this range, which makes it more difficult to specify a frequency response.

Gnatzy and Tautz (1980) investigated the oscillation amplitudes of three filiform hairs with lengths from 600 to 1000 μm, using stimuli having constant particle displacement and varying frequency. According to their figure showing the dependence of hair movement on stimulus frequency and air-particle translation (Fig. 6, Gnatzy and Tautz 1980), the sensitivity rises by ca. 30 dB per frequency decade. When converted from translation to peak air-particle velocity, this corresponds to a sensitivity increase of 10 dB per frequency decade in the range 20–200 Hz. This result is not entirely in agreement with the present findings or those of Kämper and Kleindienst (1990) and Shimozawa and Kanou (1984b), all of which indicated a less steeply rising frequency response for long filiform hairs. Kumagai et al. (1998a), however, report for 1-mm/s stimuli gain slopes of about 10 dB/decade for hairs longer than 1000 μm and much larger gain slopes for short hairs.

The frequency of maximum sensitivity found by Gnatzy and Tautz (1980) – ca. 200 Hz for filiform hairs between 600 and 1000 μm in length – is almost identical to the values calculated by Shimozawa and Kanou (1984b) while Kumagai et al. (1998a) found maximal sensitivity of those hairs at 70–120 Hz with 1-mm/s stimuli. Our present measurements did not go beyond 100 Hz and hence give

no information about resonance phenomena in the region of 200 Hz. With long filiform hairs, a slight increase in oscillation amplitude at 50 Hz was measured in the lower intensity range (10–100 mm/s). The studies of Kämper and Kleindienst (1990) confirm an oscillatory resonance of filiform hairs only in the low-frequency range, around 50 Hz. These authors also discuss the measurements of Gnatzy and Tautz (1980) and the theoretical considerations of Shimozawa and Kanou (1984b), pointing out possible reasons for the discrepancies in the results.

According to the present findings, categorizing cercal filiform hairs of crickets as predominantly velocity-oriented or acceleration-dependent populations (Shimozawa and Kanou (1984a, b) is not strictly correct. It must at least be modified to allow for transitional forms (see also the discussion by Kämper and Kleindienst 1990). Alternatively Roddey and Jacobs (1996) suggested another categorizing of filiform hairs of different length based on the frequency dependent phase shift between stimulus and response.

Our results show that the range of stimulus intensities over which the frequency response of the filiform hairs remains constant depends on the length of the hair shaft. Long hairs, being more sensitive, strike the socket and hence change their oscillatory behavior at lower air velocities than shorter hairs do. As air velocity steadily rises, the transition from unhampered hair movement through contact between the hair shaft and the ring lamella of the socket to finally tilting of the socket is not uniform. The biomechanical measurements show that, as the force exerted through the hair shaft on the socket increases, the socket at first resists displacement and then suddenly, once a certain threshold has been passed, tilts over relatively large angles. At the same time, the frequency response of the hair-shaft movement changes.

The measured dependence of angular displacement on hair-shaft length indicates that when the air-particle velocity is high, the forces opposing hair movement play an increasing role. Kämper and Kleindienst (1990), using 5-mm/s stimuli (with which the hair shafts oscillate freely), found no such dependence. In our experiments, even with stimuli at 5 m/s all hairs 500 μm or more in length are deflected by practically the same amount of stimuli. Not until the stimulus intensity is raised to 5 m/s does a clear dependence on shaft length appear. Tilting of the socket and the forces required to produce it (see Fig. 11.8) are certainly responsible for these effects at high air velocities.

The maximal angles for socket tilt found by visual inspection by Dumpert and Gnatzy (1977), 30° toward the cercus tip and 18° toward the base, have been supplemented by our present measurements of the forces acting on hair shafts deflected parallel to the long axis of the cercus. The fact that all the sockets are more easily tilted toward the tip than toward the base of the cercus, in our opinion, indicates that the membranous zone surrounding each socket is asymmetrically deformable and is characterized by a specific preexisting tension.

Furthermore, our biomechanical studies have shown that the oscillatory system comprising a filiform hair plus its socket behaves differently from the filiform hair alone as it oscillates freely in response to lower-intensity stimuli. When the

socket is indirectly tilted by the hair shaft, under the influence of sinusoidal air movement, distinct resonances appear at 10–20 Hz. The threshold for socket tilt is frequency-dependent, being particularly low (0.5–1 m/s) near resonant frequency. The relatively high air velocities (2–5 m/s) required to tilt the socket at 2 Hz are consistent with the results of direct observations of socket movement and behavioral experiments in which 1.9 m/s was found as the threshold value. Note that in Table 1 of Dumpert and Gnatzy (1977) the indicated directions of air flow are reversed; that is, in Table 1a the text "toward the cercus base" should be replaced by "toward the cercus tip", and in Table 1b "toward the cercus tip" should read "toward the cercus base".

Regardless of the preferred direction of associated filiform hair oscillation, all the hair sockets preferentially tilt in a direction parallel to the long axis of the cercus. Indeed, with the stimulus amplitudes used here they could not be tilted in the perpendicular direction (cf. Dumpert and Gnatzy 1977). As a result, the directional characteristic of the campaniform sensilla is considerably simpler than that of the cercal filiform hairs. The receptors in the campaniform sensilla can distinguish only between deflection of the socket from proximal to distal and the reverse deflection. However, due to the fact that the two cerci are set at an angle to one another, directional specificity for lateral air stimuli could be achieved by appropriate central processing.

11.4.3 Electrophysiology

Stimuli with the lowest air-particle velocities excite only the receptors in the long filiform hairs (those of hairs ca. 1000 μm in length have thresholds around 0.03 mm/s; Shimozawa and Kanou 1984a). Velocities about 100 times higher are needed for excitation of the short hairs (ca. 250 μm shaft length; Shimozawa and Kanou 1984a). Our electrophysiological experiments with high-velocity air movement have confirmed the inference, from the biomechanical measurements presented here, that above these thresholds there is only a limited intensity range within which the sensory cells of the filiform hairs optimally represent stimulus intensity in their spike activity. That is, at high intensities the number of spikes discharged by the hair receptors is reduced, evidently because the shaft of the hair is impeded in its movement by contact with the socket. This reduction in spike activity can also be observed when the hair shaft is deflected by directly pushing it. The receptors discharge while the shaft is moving, but the discharge rate drops after the shaft has struck the socket (for detailed experiments on the electrophysiology of filiform hair receptors see Weber 1990). Dumpert and Gnatzy (1977) obtained similar results by deflecting filiform hairs over large angles with high-velocity laminar airstreams. It may be that this receptor-cell phenomenon results from changes in the mechanical relationships in the tubular body (Gnatzy and Tautz 1980). From experiments with single stimuli of different temporal profiles Landolfa and Miller (1995) concluded that filiform hair receptors of the cricket respond to hair velocity but

not to constant displacement or acceleration. Also in the wandering spider *Cupiennius salei* long tactile hair sensilla primarily react to deflection velocity (Albert et al. 2001).

In contrast to our experiments and to the before mentioned studies, which used pure frequency stimuli, single pulses or air streams of constant velocity, Roddey and Jacobs (1996) applied white noise stimuli with a frequency band of 10–1300 Hz and velocities of 0.01–10 mm/s to analyze the response properties of sensory cells of cercal filiform hairs in *Acheta domesticus*. From the spike pattern of individual receptors they reconstructed the effective stimulus form, which – in the velocity domain – sufficiently matched the actual stimulus only for long filiform hairs. Short and middle hairs responded preferentially to brief components of high amplitude within the white noise stimulus. The authors found that the hair's mechanical properties establish a band pass filter so that hairs longer than 800 μm transmit frequencies up to 100 Hz, while shorter hairs are most sensitive between 150 and 250 Hz. Roddey and Jacobs (1996) conclude that receptors of short hairs code suprathreshold high frequency stimuli as binary all-or-nothing events, while those of long hairs supply also information on stimulus amplitude. This contradicts our data, as we found receptors of long hairs to encode stimulus intensity hardly or not at all, but receptors of short hairs generated more spikes with increasing air velocity. Although the findings and interpretations of Roddey and Jacobs (1996) complement our own results, they cannot be compared directly as we tested a much larger range of stimulus intensities but a lower and more restricted range of stimulus frequencies.

During sinusoidal air movement, the sense cells in filiform hairs discharge spikes in an obviously temporal relation to the stimulus up to the air velocity at which the socket limits the deflection of the hair shaft. The response of campaniform sensilla to high-intensity sinusoidal air movement is characterized by several typical features. The activity and the response thresholds of the receptor cells are strongly frequency-dependent. At 20 and 50 Hz the lowest air velocities (0.5 m/s) suffice to elicit a response, and the highest discharge rate is usually reached at high velocities and a stimulus frequency of 50 Hz.

The characteristics of the campaniform sensillum response can be explained on the basis of the biomechanical measurements and the observed socket movement. These responses differ distinctly from those of the filiform hairs, not only in their considerably higher thresholds but also in their typical frequency dependence and the intensity-dependent phase angle of the spikes.

As a filiform hair is deflected over a large angle, the campaniform sensilla coupled with it respond to the tilting of the socket. Their level of activity is related to the velocity of the socket movement. When the socket is held steady in a tilted position, the discharge rate of the sense cells in the campaniform sensilla falls off almost exponentially. These cuticular stretch receptors respond either to distal or to proximal tilting of the socket. A few exceptions may be due to mechanical interference by the tungsten recording electrode, which could change the tension in the cuticle with which it is in contact. Similar responses of campaniform sensilla were obtained by Dumpert and Gnatzy (1977) in experiments in which the socket was tilted sinusoidally by direct contact

11.4.4 Functional Aspects of the Coupling of Filiform Hairs with Campaniform Sensilla

Filiform hairs provide crickets with a highly sensitive receptor system capable of differentiating air-particle movements in the low-frequency range (2–100 Hz in our experiments), due to their diverse combinations of directional selectivity, sensitivity and frequency response. The coupling of filiform hairs with campaniform sensilla creates a composite mechanoreceptor with an extended working range, with some limitations on the precision of directional and intensity coding. In addition, the composite mechanoreceptor serves as a tactile receptor system superior in its spatial detection range (filiform hair length in *Acheta domesticus* up to ca. 1500 μm, in *Gryllus bimaculatus* up to ca. 3000 μm; Dumpert and Gnatzy 1977). Indirect stimulation of campaniform sensilla by marked deflection of the hair socket initiates various forms of cricket behavior, depending on the stimulus situation. In the presence of a high-velocity air current (> 1.9 m/s) the so-called kicking response can be observed (Huber 1965; Dumpert and Gnatzy 1977), a rapid movement with both hindlegs that is triggered by the campaniform sensilla. Crickets lacking campaniform sensilla (due to chemically induced mutations) do not exhibit this behavior (Bentley 1975).

The campaniform sensilla are also implicated in the interactions between *Acheta domesticus* and the parasitoid digger wasp species *Liris niger* (Gnatzy and Heußlein 1986; Hustert and Gnatzy 1995; Gnatzy 2001). Tactile stimulation of the cercus by the antennae of attacking female wasps elicits a defensive kick by the cricket, toward the stimulated side (see Fig. 11.1). These tactile stimuli strongly deflect individual filiform hairs. Consequently, hair sockets are tilted and campaniform sensilla are stimulated. The fact that this behavior can also be elicited by touching the filiform hairs with a fine brush confirms that the stimulus is exclusively mechanical. Crickets can also be observed to kick during aggressive behavior toward conspecifics (Alexander 1961).

When a strong puff of air strikes the cerci, the cricket jumps away (air velocity about 1 m/s; M. Hörner, personal communication). Murphey and Palka (1974) related this behavior to giant-fiber activity ("powerful stimulation of cercal receptors, which excites the giant fibres as a group, often elicits escape jumps"). It is considerably more likely, however, that the stimuli employed by Murphey and Palka (1974) were suprathreshold for campaniform sensilla on both cerci; jumping is triggered when these sensilla are excited, together with filiform hairs, by strong air stimuli. In terms of the motor events involved, this behavior can be regarded as bilateral kicking. In the locust, jumping is known to involve a motor pattern similar to that in kicking (Pflüger and Burrows 1978). The same probably also applies to the cricket, although here the motor pattern of the kick differs from that in the grasshopper (the cricket lacks the co-contraction phase of flexor and extensor; Hustert and Gnatzy 1995).

11.5 Conclusions

1. Quantified air-movement stimuli (2–100 Hz, 5–5000 mm/s; Fig. 11.4) were used to investigate the biomechanical characteristics and sensory performance of the mechanoreceptor system on the cerci of the cricket *Acheta domesticus*, each element of which consists of one filiform hair sensillum and one to three campaniform sensilla.
2. When stimulated in their preferred direction by sinusoidal air movement at low peak velocities (up to ca. 100 mm/s), the filiform hairs oscillate with velocity-correlated amplitude (see Fig. 11.4). The visually measured deflection angle and the frequency response depend on the length of the hair shaft (Figs. 11.5 and 11.6).
3. At higher stimulus intensities (200–500 mm/s) the hair shaft is deflected far enough to contact the surrounding socket. The sockets of filiform hairs with a long shaft ($> 1000\mu$m) begin to be tilted by the hair when the air velocity parallel to the long axis of the cercus reaches about 1 m/s (Figs. 11.5 and 11.6).
4. The sensory cells of the filiform hairs discharge action potentials at a constant phase with respect to the air movement when the movement velocity is low. The spike activity becomes maximal at ca. 500 mm/s (Fig. 11.11).
5. Campaniform sensilla give phasic responses to deflection of the hair socket. This receptor-cell activity is distinctly frequency-dependent; it reaches a maximum at 50 Hz, whereas the lowest thresholds are found at 20 Hz and air velocities of 0.5–1 m/s (Figs. 11.13 and 11.14).
6. Hair shafts of individual filiform hairs on isolated, unfixed cerci were manually deflected within a SEM to observe changes caused by repeated deflections in different directions. Strong deflection of the hair shaft parallel to the longitudinal axis of cercus causes tilting of the socket in which the hair shaft inserts. Also, depending on the direction of hair shaft deflection (toward the tip and/or the base of cercus, respectively) – the cuticle in the vicinity of the tilted socket is indented or arched up (Fig. 11.7). The campaniform sensilla may be effectively stimulated by these slight deformations, as they correlate qualitatively with the spike activity of the campaniform sensilla during hair deflection in different directions.

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